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Eastern Pacific tropical and subtropical decapods (Macrura; Natantia).

I. Vertical distribution and migration. A review

by

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Abstract: Only recently have extensive collections been made using trawls especially designed to sample deep-sea populations. The analysis of available information indicates that the caridean decapod biomass varies considerably in different parts of the ocean, being usually quite large at depths between 200 and 1,000 m. Among these decapods, the Pasiphaeidae, the species of *Parapasiphae* excluded, exhibit a shallower depth distribution as compared with the red-colored Oplophoridae.

A more complete understanding of the vertical distribution of caridean populations will be attained through the use of large, opening-closing, horizontally hauled, trawls capable of fishing at depths below 1,000 m in combination with sophisticated depth, dissolved oxygen, salinity, and temperature recorders.

Light, temperature, salinity, and pressure, as well as the occurrence of endogenous rhythms, are considered as the factors which could directly influence and regulate migrations. However, the occurrence of vertical migrations among quite different and unrelated groups of pelagic organisms can only be explained on the basic of the advantages (biological, ecological, genetic, trophic, and physiological) derived by panktonic and nektonic forms from these migrations.

As a result of studies dealing with the vertical distribution of pelagic crustacean populations, observations have been made on vertical migrations (diel, seasonal or ontogenetic) of marine organisms. Although several explanations have been advanced as to the causes and significance of such massive vertical movements, there are still many unanswered questions on the subject. None of the hypotheses so far seem to satisfactorily explain all the reported observations.

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VERTICAL DISTRIBUTION OF CRUSTACEAN DECAPODS

The study of available records on depth distribution of crustacean decapods shows that a considerable number of species are benthic; comparatively few populations, the holoplanktonic forms, inhabit the pelagic division. The Brachyura, Eryonidae, Paguridae, and Palinuridae, are examples of benthic crustaceans which temporarily go through a planktonic mode of life. Most species of Macrura-Natantia are among the permanent inhabitants of the pelagic environments.

Five families of the section Caridea, including nearly 50 species of shrimp, Bresiliidae, Oplophoridae, Pandalidae, Pasiphaeidae, and Physetocaridae, are known to be pelagic. Little, however, can be said about the vertical distribution from records of shrimp collected during the earlier deep-sea expeditions. The majority of the specimens examined were caught with open nets in vertical hauls and several species of pelagic shrimp were described from bottom trawl samples (3, 34). FAXON (21), RATHBUN (47), and SCHMITT (54) reported on the caridean and penaeidean shrimp collected from the north eastern Pacific by the ALBATROSS. However, most of these collections were made with bottom trawls on the continental shelf, therefore it is impossible to infer anything about the distribution of the oceanic species.

STEPHENSEN (5), in his systematic treatment of the Macrura collected by the THOR expedition, included valuable information on the vertical distribution of caridean decapods. Two species belonging to the genus *Pasiphaea,* found at night almost exclusively in the upper 300 meters, were only caught at considerable depths during the day. Another pasiphaeid, *Parapasiphae sulcatifrons,* was always captured below 1,000 m. One species of *Acanthephyra,* was not captured above 300 m at night and only appeared in samples taken below 1,000 m during the day. *Hymenodora gracilis* was found to migrate from 1,500 to 750 m, remaining during the day in the lower 500 m of its range. *Hymenodora glacialis* was relatively common in samples taken below 1,000 m. WELSH, *et al.* (61), reported on the vertical distribution and migration of two species of Oplophoridae taken in the Sargasso Sea with large, horizontally hauled, closing nets. Diel vertical movements of over 400 m, with daytime depths of 800 m or more, were found for *Acanthephyra purpurea* and *Systellaspis debilis.* WATERMAN, *et al.* (58), working off Cape May, N.J., and using the same type of gear, obtained serial samples from seven different depths, between 100 and 1,200 m. Two oplophorids, *Hymenodora glacialis* and *Acanthephyra purpurea,* were captured in large numbers: *Hymenodora glacialis* was not caught during daytime in waters above 800 m and the range of its vertical migrations was found to be approximately 200 m; *A. purpurea* was found to perform extensive diel migrations of nearly 600 m. One pasiphaeid, *Parapasiphae sulcatifrons,* was also captured in large numbers and found to migrate from daytime depths of nearly 800 m to a nighttime level of 400, with juvenile forms moving into the upper mesopelagic zone. Only recently have extensive collections been made using trawls especially designed to sample pelagic populations, e.g., the Isaacs-Kidd Midwater Trawl (28).

Available information can be used to describe in general terms only the vertical distribution of caridean populations in very limited areas of the oceans.

VINOGRADOV (57), using the data from material collected during the cruise of the VITYAZ to the northwestern and equatorial parts of the Pacific Ocean, concludes that the decapod biomass varies considerably in different parts of the ocean, being usually quite large at depths between 200 and 500 m. The maximum depth recorded for caridean shrimp in the subpolar regions of the northwestern part of the Pacific were approximately 5,000 m for *Hymenodora glacialis* (57). *Hymenodora frontalis,* one of the abundant forms, lives at depths between 750 and 1,500 m in the Kurile-Kamchatka area, while juvenile forms occur between 200 and 500 m.

Limited information is available from the northeastern part of the Pacific Ocean. PEARCY and FORSS (45), with a modified six-foot Isaacs-Kidd Midwater Trawl, took oblique hauls between the surface and 1,000 m and found that no adult caridean forms live exclusively in the upper 200 meters. Two species of the genus *Pasiphaea, P. pacifica* and *P. chacei,* were captured within the epipelagic zone only at night. The oplophorids, *Hymenodora frontalis, H. gracilis,* and *Systellaspis braueri,* were most abundant in the upper mesopelagic waters. *Notostomus japonicus* and *Acanthephyra curtirostris* were never caught in the upper 200 m. *Parapasiphae sulcatifrons* and *P. cristata* were always restricted to depths between 500 and 1,000 m. Little information is included regarding diel movements of these large nektonic shrimp, mainly because they were caught in small numbers. MURILLO (40) studied the depth distribution of 16 species of caridean decapods belonging to seven genera, *Pasiphaea, Parapasiphae, Glyphus, Hymenodora, Acanthephyra, Systellaspis,* and *Notostomus,* taken off southern and Baja California. The results of these studies will be reported in future papers.

Because of both the lack of large collections taken at discrete depths and the fact that most of the available midwater-trawl material has been captured at depths not exceeding 1,000 m, the lower limits of the vertical distribution of many bathypelagic shrimp populations are still unknown.

In order to clearly understand the vertical distribution of midwater populations future research should emphasize the use of opening-closing, horizontally hauled, trawls capable of fishing below 1.000 m as that now under experiment at the Allan Hancock Foundation of Southern California (unpublished results).

VERTICAL MIGRATION

Accounts on vertical migration of planktonic and nektonic organisms began appearing following the British CHALLENGER expedition. FUCHS (24), reporting on the material collected during this expedition, stated that crustaceans, among other animals, return to the dark, deep waters during the day. MURRAY (41) was the first to realize the extent of these migratory movements and suggested that some organisms living at various depths down to and even deeper than 200 m migrate toward the surface. Hjort (MURRAY and HJORT, 42) was able to detect changes in the depth distribution of several decapod species performing vertical migrations from daytime depths of 800 m or more. ESTERLY (19) investigating the vertical distribution of several species of copepods, indicated that vertical migrations occurred from depths of 400 m. BODEN (7) and BRINTON (9) recorded extensive migrations of several species of euphausiids off southern California. BRUSCA (10) reported on the vertical movements of some gammarid amphipods in waters over the Santa Catalina Basin, off southern California. PEARCY and FORSS (45) presented data on the vertical distribution and migration of several oceanic shrimp populations off the central Oregon coast.

BRADFORD (8) recorded vertical migratory movements of several species of copepods off eastern New Zealand. FOXTON (22) and VIVES (58) reported on the vertical distribution and diel migrations of natant decapods and copepods, respectively, in the eastern Atlantic Ocean. MORAITOU-APOSTOLOPOULOU (37) analyzed the characteristics and intensity of the vertical movements of several copepod species taken in the Mediterranean Sea. ROGER (49) divided the euphausiid species collected in the equatorial Pacific Ocean into four main types acoording to their vertical distribution and described their migratory habits.

As more information accumulated it became clear that the most active migrators belonged to the nekton, the movements along the water column not being confined to the epipelagic zone. Many deep-sea animals regularly change their depth, the extent of their vertical displacements generally varying during their ontogeny. This activity, consisting of a nighttime rise followed by a daytime descent, has been termed "diel vertical migration" and is regarded as a normal behavioral pattern for most pelagic organisms (4).

The available literature on vertical migration is both extentive and controversial. Many explanations, mostly speculative, have been advanced regarding the causes, mechanisms involved, and the adaptive significance of these vertical movements. Despite the attention devoted to it, the phenomenon is still poorly understood. Among the controversial issues is that of the conditions determining diel and other vertical migrations. The lack of understanding comes in part from the fact that there has not always been a clear distinction between the basic aspects of the phenomenon, mainly the factors determining the vertical movements, and the adaptive value or biological advantages derived by planktonic and nektonic populations from these vertical movements. The factors which can directly influence and regulate vertical migration have received a great deal of attention. CUSHING (14), BAINBRIDGE (2), PERES and DEVEZE (46), RAYMONT (48), BANSE (4), MILLER (36) and VINOGRADOV (58) commented on several aspects of vertical distribution and vertical migration of planktonic and nektonic organisms and the parameters considered as important.

Changes in temperature of the upper layers were considered by CHUN (11) to be the cause of migrations. Even if valid for the near surface plankton, this explanation does not account for the movements of those organisms living below the thermocline, where daily temperature changes, if any, are very slight. Temperature, however, appears to be an important factor that limits the extent of these vertical movements (39). The possible role of pressure as an important factor was advanced by PARKER (44) and ESTERLY (19). More recent investigations have failed to find any relationship between vertical migration and pressure alone (2). EYDEN (20) suggested that downward movements in the epipelagic zone are caused by cyclic changes in specific gravity. This idea was criticized by GARDINER (25), who demonstrated that migrants were incapable of attaining the rate of sinking known in migrations if they depended only upon gravity. The existence of physiological diel rhythms was proposed by CLARKE (12) and the idea reviewed by HARRIS (27). RUTJACOV (51), based on experiments carried out with anaesthetized zooplankters, considers that downward migrations of planktonic populations may be entirely attributed to passive sinking. His evidence favors the supposition that diel vertical migration results from an innate alternation of phases of high and low locomotory activity. BACKUS, *et al.* (1) suggested that the direct influence of light constitutes a stronger stimulus than the endogenous diel rhythm.

Ever since serious studies of vertical migration began, light has been assumed to play a very important role as a triggering factor. Beginning with WEISMANN (60) most of the early works emphasized the adaptation of the migratory organisms to specific values of light intensity. ROSE (50) demonstrated the existence of zones of optimum light intensities in the oceans. RUSSELL (52, 53) provided positive evidence supporting the role of light as a major factor regulating migrations. From his experimental work Russell concluded that pelagic populations concentrate in zones of optimum illumination. Diel changes in light intensity cause the populations to move vertically, descending when light intensity increases or ascending when the intensity decreases. More recent experimental work provides additional evidence as to the importance of light as a triggering factor in vertical migration. HARDY and BAINBRIDGE (26) and DIGBY (17) indicated that different species have different light intensity preferences.

With nektonic Crustacea participating in diel movements extending from 200 to 600 or even 1,000 m, a number of questions are raised, mainly with respect to light penetration in the oceans and the ability of deep-sea organisms to detect very low light intensities. Using photographic plates, MURRAY and HJORT (42) were able to detect light at depths below 500 m. CLARKE and HUBBARD (13) found that the greatest depths at which day-night changes in illumination could be detected were from 700 to 1,000 m. Additional evidence in support of the important role played by diel changes in illumination in the vertical movements of nektonic populations came from the discovery of the deep scattering layers, DSL's, which are broad zones of diffuse accoustic reverberation recorded on echo sounders at mid-depths. DIETZ (16) was able to show the presence of almost ubiquitous, discrete scattering layers throughout the temperate oceans of the world. These occur roughly between 230 and 800 m during the day and rise almost to the surface at night, where they diffuse or merge into a broad band of approximately 200 m. It was soon suggested, and later confirmed, that these discrete layers were nothing but aggregations of deep-sea organisms living in deep, dimly-lit waters in daytime and ascending only at night to browse in the rich upper layers. Evidence gathered from several studies before 1962 tend to indicate that the predominant organisms in these layers were myctophids, sergestids, and euphausiids. The organisms may be taken in the near-surface waters at night and at the very surface during dark nights. BARHAM (5), reporting on his direct observations of DSL's from the bathyscaphe TRIESTE off San Diego, California, indicated a somewhat different composition of the scattering layers, with physonectia siphonophores showing the best and most consistent spatial relationship with the DSL's, euphausiids being common in the upper layer, and sergestids in the lower component of the DSL's. Lantern fishes were observed only well below the recorded scattering layers. Reporting on some recent observations aboard the SOUCOUPE, BARHAM (6) found a significant difference in the composition of the DSL's off Baja California with myctophids occurring in large quantities on top of the main scattering layer. VIVES (58) suggests that copepods could also be among the important contributors to the deep scattering layers. KAMPA and BODEN (30), studying light generation in a sonic scattering layer off southern California, found a close correlation between DSL's and bioluminescence, suggesting that luminescent activity actually increases during the periods of vertical migration. VINOGRADOV (57) observed that just before dawn the near-surface bulk of nektonic organisms initiates its descent, soon breaking into several discrete bands according to optimum light values for every species, the vertical spread of a population being attributed to differences in optimum light according to age and physiological state of the organisms. MOORE and CORWING (38) experimentally showed that the effect of illumination and temperature on migration changes with depth. Their results seem to indicate that migrations are the consequence of the combined action of light, temperature, and pressure. Small organisms, e.g., crustaceans, although lacking a gas bladder, are apparently capable of sensing changes in pressure because of their specific compressibilities, which are 15 to 40% lower than that of the surrounding water (18). Despite the available evidence in support of light as the most important stimulus for the diel vertical migrations, and of its combined action with temperature, salinity, and pressure, none of these factors or combination of them can satisfactorily explain the widespread occurrence of the phenomenon. We are, therefore, led to suspect that vertical migration is in essence an adaptation developed and established through the process of evolution. Its ocurrence among quite different and unrelated groups of pelagic organisms can be explained only on the basis of the advantages derived by plankton and nekton from these migrations.

Several hypotheses have been advanced by students of vertical migration in attempting to explain its biological advantages. It has been suggested that the adaptive value of diel vertical migration is the protection of herbivorous zooplankters from predators during daytime in the upper layers. This idea, held by several Soviet authors (KOSHOV, 31; NIKOLAEV, 43; MANTEIFEL', 35), sounds reasonable in the case of certain zooplankters undertaking extensive diel migrations, *e. g., Sergestes similis* (45), but does not seem to be applicable in cases of organisms migrating very short distances both in the upper and lower portions of the pelagic division. The adverse effect that the short wave components of solar radiation could have on planktonic organisms, if continuously exposed, has also been used by some authors to explain the adaptive value of the daytime sinking of populations living in the surface waters (29, 56). The hypothesis that vertical migrations facilitate the exchange of genetic material by bringing conspecific populations in close proximity to each other has been advanced by DAVID (15). According to him, through migrations populations maintain a constant flow of hereditary material, increasing the possibilities for mutation and recombination, eventually promoting variability and reducing the chances of becoming isolated. This would lead to enrichment of the gene pools of the populations involved, increasing the possibilities of surviving drastic environmental changes. Vertical movements through different types of water could also aid in the preservation of, and even facilitate the expansion of, the range occupied by a population. On the other hand, with surface and deeper waters often moving in opposite directions, vertical migrating organisms are horizontally transported back and forth, the net result being that populations tend to remain in the same general area. MACKINTOSH (33) believed this to be the case in the Antarctic Ocean.

MCLAREN (32), in a review of the effects of temperature on the growth of zooplankton, offers an alternative explanation for the adaptive value of vertical migration in thermally stratified waters. Light and temperature play an important role in controlling vertical movements. Migratory organisms are active in the warm, energy rich, and dangerous upper waters during the nighttime, descending to the energy-poor, cooler and darker waters during the day. MacLaren suggests that the adaptive value consists in the energy "bonus" saved by the organisms, most of the metabolic processes of which take place in waters of low temperatures. The energy thus saved could then be invested in reproduction. This idea, however, does not account for migrations reported from oceans with colder surface waters and warmer underlying ones, as is the case in the Antarctic Ocean (23, 33). RUTJACOV (51) suggests that vertical migrations are not the result of an adaptation to the planktonic mode of life but the consequence of an evolutionary trend towards the reduction of energy expenditure for the maintenance of the body in a suspended state, i.e., neutral buoyancy.

FINAL REMARK

Finally, although none of the above mentioned ideas satisfactorily explains the widespread occurrence of vertical migrations (diel, seasonal or ontogenetic), and although each hypotehsis accounts for only some of the patterns known to occur, usually on the basis of observations on particular populations in a particular area, during the past decade there has certainly been remarkable progress towards the understanding of the dynamics of pelagic populations. The most probable explanation for the common occurrence of migration in waters of all the oceans lies in a combination of all or most of the factors taken under consideration so far, mainly: a) biological, allowing pelagic populations to disperse along the water column according to their internal structure (i.e., sexes and/or developmental stages); b) ecological, the populations moving between, and entering, rather different species assemblages; c) genetic, stimulating the exchange of genetic material by bringing conspecific populations in close proximity to each other; d) trophic, allowing the active transport of nutrients between the energy-rich epipelagic waters and the impoverished deep regions of the oceans; e) physiological, migrant populations by remaining in cool-dark waters during daytime save an energy "bonus" which could then be invested to insure reproductive success of the species.

RESUMEN

La mayor parte de la información acumulada durante las primeras expediciones oceanográficas es de valor limitado en la interpretación de la ecología de las poblaciones de camarones pelágicos, aunque de importancia desde el punto de vista descriptivo. No ha sido sino recientemente que se han obtenido muestras adecuadas de organismos pelágicos con redes especialmente diseñadas para pescar a profundidad en aguas abiertas. El análisis de la información hasta ahora acumulada indica que la biomsa de decápodos carídeos se encuentra principalmente entre 200 y 1000 m aunque varía considerablemente en diferentes partes del océano. Entre estos crustáceos, los que pertenecen a la familia Pasiphaeidae, con excepción de las especies del género *Parapasiphae,* habitan aguas menos profundas que aquellas ocupadas por los camarones rojos de la familia Oplophoridae.

Con el propósito de lograr un claro entendimiento de la distribución vertical de estas poblaciones pelágicas, se insiste en la necesidad de usar redes grandes, equipadas de tal manera que puedan ser manipuladas desde cubierta (abrirse y cerrarse), especialmente diseñadas para pescar eficientemente a profundidades superiores a 1,000 m. Estas redes deberían usarse en combinación con instrumentos capaces de transmitir información sobre profundidad, oxígeno disuelto, salinidad, y temperatura.

La luz, la temperatura, la salinidad y la presión, lo mismo que la existencia de ritmos endógenos, son considerados como los factores que podrían determinar y regular directamente las migraciones verticales. Sin embargo, el hecho de que éstas sean características de tantos grupos diferentes de organismos pelágicos, sólo puede explicarse con base en las ventajas biológicas, ecológicas, genéticas, tróficas y fisiológicas derivadas de estos movimientos verticales por los organismos planctónicos y nectónicos.

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