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Principal Investigator: ¹⁰ Dr. Robert Y. George

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water crustaceans show a very pronounced convulsive reaction and beyond 200 atm there is evidence of well defined inhibitory effects of pressure leading to paralysis of the experimental animals. This high pressure inhibition threshold level at 200 atm corresponds with earlier studies revealing inhibitory effects on nerve conduction, enzyme inactivation, and other biochemical changes involving protein structure.

It is of interest to find out that low temperature acclimation appears to have an antagonizing effect and therefore, the hyperactivity syndrome as well as the convulsive reactions while under the influence of pressure becomes very less dramatic in crustaceans acclimated to low temperature for long periods (3 months or more).

Another important finding resulting from this contract deals with the pressure responses of scavenging deep sea amphipods that occur at depths exceeding 2000 m. These amphipods were trapped and retrieved alive with adequate temperature control. In the laboratory the metabolic rate and ventilation frequency of pleopods were monitored at seven different pressure levels between 1 atm and 325 atm. These results pointed out that pressure does not significantly influence the metabolic activity of this deep sea amphipod.

INTRODUCTION

This final technical report represents the completion of a research project that dealt with the influence of hydrostatic pressure on the behavioral and metabolic activities of crustaceans inhabiting the upper slope depths in the abyssal environment. The study emphasized live retrieval of deep sea animals under conditions of controlled temperature. Successful recovery of upper abyssal animals was accomplished by conducting retrieval studies in the winter months off North Carolina when the water column lacked a pronounced temperature gradient and by immediate transfer of deep sea animals into a temperature-controlled laboratory on board the ship. Live retrieval studies were also conducted in the high latitude marine environment where isothermal conditions prevail.

Pressure chambers were used to simulate deep sea conditions to observe the behavior and monitor metabolic rate of these organisms when compressed back to their normal high pressure habitat conditions. The method also involved a series of long term deep sea simulation experiments in the shore laboratory at the Institute for Marine Biomedical Research where the use of the Mark III high pressure aquarium system enabled the investigator to perform experiments under selected pressures for periods as long as two weeks.

In these long term experiments, deep sea crabs were maintained at 100 atm and 150 atm, 250 atm for 14 days. During this period it was possible to videotape the behavioral activities of the experimental animals and also monitor the respiration of the crabs at regular intervals by drawing water samples without any loss of hydrostatic pressure. The experimental procedure also permitted oxygenation of the system to saturated levels when the oxygen pressure dropped below 4 ppm. This high pressure aquarium system was outfitted with a polarographic oxygen electrode for continuous recording of

oxygen tension and with thermistors for uninterrupted recording of chamber temperature. Over seventy high pressure experiments were performed with deep sea crabs and amphipods. The results are now published in papers that constitute an integral part of this final report.

Major findings resulting from this ONR contract:

Recent research on high pressure adaptations point out that there is a definite metabolic change when organisms are subjected to increasing hydrostatic pressure. In the model depicting responses of shallow water crustaceans, a pronounced increase in locomotor activity is seen as a hyperactivity syndrome at pressures ranging between 50 and 80 atm. This stimulatory effect of pressure also induced an intermittent increase in metabolic activity. At pressures ranging from 100-150 atm these shallow water crustaceans show a very pronounced convulsive reaction and beyond 200 atm there is evidence of well defined inhibitory effects of pressure leading to paralysis of the experimental animals. This high pressure inhibition threshold level at 200 atm corresponds with earlier studies revealing inhibitory effects on nerve conduction, enzyme inactivation, and other biochemical changes involving protein structure (Hochachka 1975).

It is of interest to find out that low temperature acclimation appears to have an antagonizing effect and therefore, the hyperactivity syndrome as well as the convulsive reactions while under the influence of pressure becomes very less dramatic in crustaceans acclimated to low temperature for long periods (3 months or more). The results of this investigation constituted part of the following paper: George, R.Y. 1979. What Adaptive Strategies Promote Immigration and Speciation in Deep Sea Environment. *Sarsia* 64(1-2): 61-65. (Please see Appendix 2).

The studies on the upper abyssal slope crab, Parapagurus pilosimanus revealed a pattern of response strikingly different from that of shallow water crabs. These deep sea crustaceans did not exhibit any hyperactivity when subjected to increasing pressure. However they exhibit convulsive reactions at much higher pressure levels in comparison with their shallow water counterparts. Prolonged acclimation of these crabs at 1 atm modified the pressure responses that characterise these crabs soon after capture. In other words crabs acclimated at 1 atm for periods extending three months behaved very much like shallow water crabs on exposure to increasing pressure. This behavior suggests the phenotypic nature of pressure responses. The metabolic activity of Parapagurus pilosimanus did not show any pronounced variation under their normal physiological range of pressure (60-200 atm). However these deep sea crabs showed a marked increase in activity, metabolism and food consumption when acclimated to increasing temperature up to 16°C. The results of this study constituted part of a publication listed below: George, R.Y. 1979. Behavioral and Metabolic Adaptations of Polar and Deep Sea Crustaceans: A Hypothesis Concerning Physiological Basis for Evolution of Cold Adapted Crustaceans. Bull. Biol. Soc. Wash., #3, pages 283-296 (Please see Appendix 3).

Another important finding resulting from this contract deals with the pressure responses of scavenging deep sea amphipods that occur at depths exceeding 2000 m. These amphipods were trapped and retrieved alive with adequate temperature control. In the laboratory the metabolic rate and ventilation frequency of pleopods were monitored at seven different pressure levels between 1 atm and 325 atm. These results pointed out that pressure does not significantly influence the metabolic activity of this deep sea amphipod. The results of these experiments became part of a recent paper

entitled "What Adaptative Strategies Promote Immigration and Speciation in Deep Sea Environment", *Sarsia* 64: 61-65.

In addition to laboratory experimental studies, this investigator also collaborated with Dr. Emilliani at the University of Miami to study the growth rate of deep sea corals in comparison with shallow water corals.

Carbon and oxygen isotope analysis through a 30-year (1944-1974) growth of Montastrea annularis from Hen and Checkens Reef (Florida Keys) shows a strong yearly variation in the abundances of both carbon-13 and oxygen-18 and a broad inverse relationship between the two isotopes. Normal annual dense bands are formed during the summer and are characterized by heavy carbon and light oxygen. "Stress bands" are formed during particularly severe winters and are characterized by heavy carbon and heavy oxygen. The isotopic effect of Zooxanthellae metabolism dominates the temperature effect on the oxygen-18/oxygen-16 ratio. The isotopic results on the deep sea solitary coral Bathypsammia tintinnabulum, where Zooxanthellae are nonexistent, indicates that the abundance of the heavy isotopes carbon-13 and oxygen-18 is inversely related to the growth rate, with both carbon and oxygen approaching equilibrium values with increasing skeletal age. The results are published in *Science* Vol. 202: 627-629 (Please see appendix 4).

In addition to the results reported above, field retrieval studies conducted in the ultraabyssal depths of the Puerto Rico Trench in two cruises of R/V GILLISS revealed the presence of wood-infesting and boring organisms and absence of biofouling organisms at depths exceeding 7000 meters. The results of these investigations are reported in a recent publication listed below: George, R.Y. and R.P. Higgins. 1979. Eutrophic Hadal Benthic Community in the Puerto Rico Trench. AMBIO 6: 51-58 (Please see appendix 5).

In summary, this research supported by ONR provided physiological data to establish well-defined differences in adaptive strategies between shallow and deep sea organisms. The results emphasise the importance of pressure as a significant environmental factor that exerts pronounced effect on the life processes in the deep ocean. On the basis of these results, this investigator is now preparing plans for further studies under ONR sponsorship to elucidate pressure-dependent life processes in the abyssal environment.

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WHAT ADAPTIVE STRATEGIES PROMOTE IMMIGRATION AND SPECIATION IN DEEP-SEA ENVIRONMENT

ROBERT Y. GEORGE

GEORGE, ROBERT Y. 1979 05 31. What adaptive strategies promote immigration and speciation in deep-sea environment. *Sarsia* 64:61-65. Bergen. ISSN 0036-4827.

Deep-sea fauna is undoubtedly composed of species that are specially adapted in the course of evolution to cope with high hydrostatic pressure. Despite our knowledge on the community structure of the deep-sea benthos, modern deep-sea biologists have not yet critically posed the question: What adaptive strategies promote immigration and speciation in deep-sea environment? This paper brings into focus the metabolic adaptive patterns that seem selectively favourable for physiological accommodation in high-pressure environment.

Experimental data on the effect of pressure on the Arctic shelf amphipod *Anonyx mugav* suggest that pressure inhibits metabolic rate at about 150 atm which is equivalent to 1500 m that corresponds with the maximum depth of inhabitancy. Pressure tends to enhance metabolic rate at moderate hyperbaric levels (10 to 120 atm) and this stimulatory effects is somewhat pronounced at higher temperature. Another adaptive strategy of pressure-independent metabolism is seen in the vertically migrating deep-sea amphipod *Eurythenes gryllus*. Deep-sea decapod *Parapagurus pilosimanus* from 1000 m exhibit convulsive episodes at 220 ± 10 atm, suggesting pressure-induced physiological trauma. Reduced metabolic rate in the lethargic deep-sea animals implies low energy input and possibly this adaptive strategy is a catalytic force in the successful colonization of high pressure and low temperature biosphere of pronounced food deficiency.

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INTRODUCTION

The deep-sea environment, that occupies the sea-floor depths from the upper Continental slope to the trench floor, is inhabited by a diverse array of metazoans of which groups such as the peracarid crustaceans are very speciose and some other groups such as the decapod crustaceans and fishes are impoverished in the abyss. Evidently the successful colonizers of the deep sea are so adapted in the course of evolution to cope with lightless conditions, low temperature, low energy flux, high hydrostatic pressure, and a seasonless contancy. Physiological theories, based upon the enormous bulk of experimental data on estuarine and shallow marine animals, offer plausible explanations for the osmotic or ionic regulations and thermal adaptations that primarily govern the distribution of these coastal organisms. On the contrary, due to the paucity of experimental data, our understanding of the adaptive strategies of abyssal animals revolves on very few physiological studies on deep-sea organisms (JANNASCH & al. 1971; GEORGE & MARUM 1974; SMITH & HESSLER 1974; MACDONALD 1975; HOCHACHKA 1975; GEORGE 1978).

The occurrence of distinct vertical assemblages of species in the deep sea and trenches (SANDERS & al. 1965; GEORGE & MENZIES 1972; MENZIES & al. 1973; BELYAEV 1966) clearly point out that certain factors obviously limit vertical distribution of species in these stable abyssal habitats. Although intensity of ambient light decreases in the upper layers of the deep sea, aphotic condition is virtually the case throughout the abyss. Eyeless conditions are commonly seen in the abyss and incidence of bioluminescence prevails to facilitate intraspecies communication, food procurement, and escape behavior against predators. The low food availability in the abyss has also induced reduced metabolic states. However, the adaptations to darkness and hypocaloric conditions are not unique to deep-sea animals since cave-dwelling animals exhibit similar adaptive strategies. On the contrary, hydrostatic pressure is undoubtedly a unique environmental parameter in the deep sea although it was presumed that pressure has a less significant influence on abyssal life than temperature (BRUUN 1957) and only in recent years pressure adaption of deep-sea animals is seriously recognized.

Deep-sea temperature is generally low (less than 4 °C) except in the Mediterranean abyss and in the vicinity of hydrothermal vent areas near the Galapagos Islands. These warm deep-sea conditions are atypical because the abyssal condition is a combination of high pressure and high temperature. Special adaptive strategies are evidently required to live in such conditions where enhanced metabolism is inevitable. Unfortunately we lack data to support such a hypothesis. In the hydrothermal vent regime, however, instability in terms of thermal and chemical environment is generally the rule. Furthermore, high H₂S levels and low oxygen content exert significant impact on the prevailing biota that largely include opportunistic species, including the giant mussels (ROWE pers. comm.) that flourish by subsisting on the enormous food concentrations of sulphur-reducing bacteria.

In the typical deep-sea environment, low-temperature conditions have exerted profound effect on the metabolic rate of the 'lethargic' abyssal animals (SMITH & HESSLER 1974; GEORGE 1979) that show relatively low rates of oxygen consumption in comparison with their shallow-water counterparts. The question that still remains unresolved, is the interaction of pressure and low temperature. In the present paper, special effort is made to focus on the effect of pressure in relation to temperature on the metabolic rate of shallow- and deep-sea crustaceans and to point out key strategies that promote colonization of the deep-sea environment.

MATERIAL AND METHODS

The metabolic responses of three species of crustaceans are considered in the present study: 1) The shelf amphipod *Anonyx nugax* from the Arctic Ocean off Point Barrow, Alaska, 2) The abyssal amphipod *Eurythenes gryllus*, from the central Arctic Basin in the vicinity of the Alpha Ridge, and 3) the bathyal anomuran decapod *Parapagurus pilosimanus*, captured from the upper slope depths off North Carolina. The shallow-water amphipods were captured with baited traps. The abyssal amphipods were collected from the Ice Island T-3 at a depth of 1850 m with the use of baited traps that were suspended with hydrographic wire approximately 1 m above the sea floor while the Ice Island remained stationary. The upper abyssal-bathyal decapods were collected from 800 to 1200 m with the use of a small biological trawl that is outfitted with a nylon net (1 cm mesh) and an insulated cod-end capsule. Populations of the above three species were carefully maintained alive for over three months in temperature-controlled aquaria.

The amphipods were exposed to high pressure in the observation chamber that was described by

MENZIES & al. (1974). The large decapods were maintained in simulated deep-sea pressure in a large volume (4.8 l) high-pressure aquarium that is built upon the concept of a double lumen envelope (BRAUER & JORDAN 1972) and is briefly discussed by GEORGE & LILYQUIST (1979). The respiration of these crustaceans under pressure was monitored both by an YSI-oxygen electrode system and by microwinkler analysis of water samples drawn from the pressure chamber at regular intervals. The experimental animals were observed and photographed with a TV camera during the course of the experiment. The compression rate in this study was 4 atm/min and at selected pressure levels, the experimental animals were maintained for a period of four hours for measurement of oxygen consumption rate.

RESULTS AND DISCUSSION

Responses of the shallow-water amphipod Anonyx nugax

These amphipods were compressed at three different temperatures, -1°, 6°, and 14 °C. Between 60 and 70 atm, the amphipods showed very excited swimming activity that was very pronounced in the higher temperatures (6 and 14° C) but somewhat less traumatic at -1 °C. A hyperactivity phase under moderate pressure levels was earlier described for shallow-water crustaceans (MENZIES & GEORGE 1972; GEORGE & MARUM 1974; MACDONALD & TEAL 1975). At 140 ± 5 atm, the amphipods showed signs of severe body jerks and flexing of legs as symptoms of the high-pressure neurological syndrome (HPNS). This convulsive episode of amphipods was considerably depressed in the low temperature (-1° C). It appears that low temperature tends to reduce the intensity and frequency of the convulsions that are induced by high pressure. In other words, the amphipods show insignificant behavioral responses to high pressure in low temperature but they are very sensitive to high pressure at higher temperatures. Beyond 150 atm, the amphipods showed signs of reduced activity and at pressures exceeding 200 atm, the amphipods were completely paralyzed. The paralysis was observed at 200 ± 5 atm in all three test temperatures.

For the purpose of determining the impact of pressure on the metabolic rate of these shallow-water amphipods, experiments were conducted at 1, 60, 140, 200, and 250 ± 10 atm to measure the rate of oxygen uptake in the three selected test temperatures. The results of this study are presented in Fig. 1. The data suggest that pressure has a stimulatory effect on the metabolic

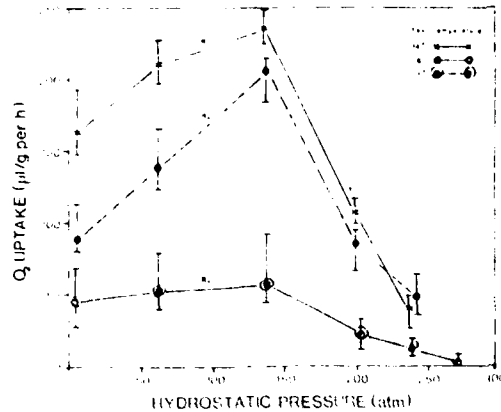


Fig. 1. Metabolic rate of the shallow-water amphipod *Amonyx mugax* to pressure and temperature. R₁ indicates the convulsion threshold. T means the onset of paralysis.

rate at 6° and 14° C but the stimulatory influence is masked by low temperature (-1° C) in hyperbaric conditions. The inhibitory effect of pressure on metabolic rate beyond 150 atm is evident in all three temperatures. It is of interest to note that this amphipod was found to be eurythermal and was easily acclimated to a wide range of temperature. Nevertheless, the behavioral and metabolic responses varied significantly between warm (> 6° C) and cold (< 2° C) conditions of acclimation. Higher tolerance to pressure and relatively insignificant metabolic effect of pressure in low temperature may offer explanations for the phenomenon of the so called eurybathiality or polar submergence phenomenon that involves immigration of species to deeper depths in the cold high latitude marine environment (GEORGE 1977).

Responses of the abyssal amphipod *Eurythenes gryllus*

The second set of experiments deals with a cosmopolitan deep-sea amphipod that occupies a wide vertical depth range from 1000 to 6200 m (BARNARD pers. comm). The test population of amphipods was captured from 1850 m and successfully acclimated at 1 atm.

These deep-sea amphipods were found to be extremely sensitive to temperature increase and showed high mortality above 4° C. The behavioral and metabolic responses of this amphipod were therefore studied under pressure at

2° C. In Fig. 2 the metabolic rate and pleopod activities are shown in relation to pressure. The data pointed out that pressure did not influence significantly the activity or the metabolic rate. The mean resting metabolic rate ranged between 60 and 64 µl/gm per h over a wide pressure range from 1 to 325 atm. In direct contrast to the shallow-water amphipod, the deep-sea amphipod did not exhibit any hyperactivity or excited behavior on exposure to pressures beyond the habitat pressure (180 atm). This observation suggests that *E. gryllus* is physiologically adapted to withstand a wide variation in pressure. These abyssal amphipods, however, showed convulsive reactions at a pressure of 520 atm that is about 340 atm above the pressure of depths at which they were captured.

The rate of oxygen consumption of the abyssal *E. gryllus* at 2° C in different pressure is about the same as that of the shallow-water amphipod *A. mugax* at -1° C. This finding is in contrast to the hypothesis that deeper-living crustaceans consume oxygen at a much lower rate (CHILDRESS 1977). Perhaps this depth-rated metabolic decline is only seen in deep-living species that are lethargic and in those species that occupy the oxygen minimum zone in the abyssal depths. The scavenging amphipod *E. gryllus* is an active swimmer and its resting respiratory rate is the same as that of shallow-water amphipods. In recent years, there have been new data to show that opportunistic organisms such as the deep-sea borers (TURNER 1973) and gut-inhabiting bacteria in the abyssal amphipods (SCHWARZ & al. 1975) have a higher growth and metabolic rate.

Responses of the archibenthal crab *Parapagurus pilosimanus*

A third set of experiments deals with a deep-sea hermit crab that occurs between 800 and 3200 m on the Continental slope environment of the North Atlantic Ocean. The crabs were captured alive at 1000 m and were acclimated and maintained at 1 atm for over a period of one year during which they showed normal reproductive activities. The effect of pressure on the metabolic rate of *P. pilosimanus* at 6° C is shown in Fig. 3. The data revealed that pressure between 1 and 100 atm has a stimulatory effect on oxygen consumption rate but pressures between 100 and 200 atm did not show significant effect on meta-

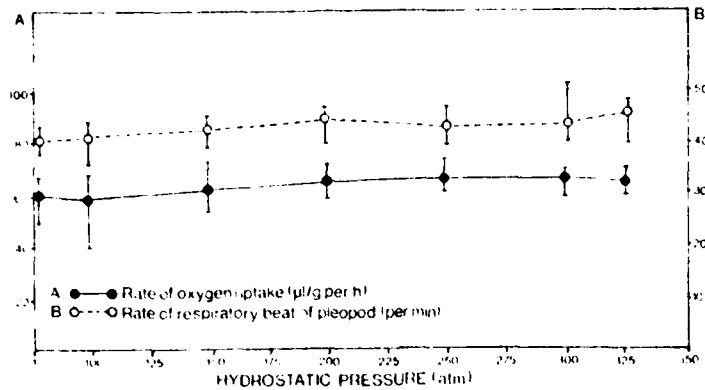


Fig. 2. Metabolic rate and pleopod activity of the deep-sea amphipod *Eurythenes gryllus* at different levels of hydrostatic pressure at 2°C.

abolic rate. It is also of interest to note that the resting metabolic rate of this 'lethargic' crab is about one third of that of the deep-sea amphipod. Here again, this low rate is attributed to the low level of activity of this crab both at 1 atm and at simulated habitat pressure. This crab showed convulsions at 220 atm that proved to be 300 atm less than the level of convulsion threshold for the abyssal amphipod *E. gryllus*.

CONCLUSIONS

In summary, I propose that the pressure response patterns of the above three crustaceans represent three distinct models of adaptive strategies. The first model is an example of pressure-sensitive species that show stressful and excitatory activities on exposure to moderate pressure and therefore are not adapted to immigrate into the abyss. The second model, as exemplified by *E. gryllus*,

represents a successful deep-sea colonizer that is metabolically insensitive to a wide range of pressure. The third model is seen at the example of *P. pilosimanus* that is only adapted to a moderate pressure range (less than 200 atm) and this crab has successfully invaded only the upper abyssal zone.

All this information confirms that pressure is evidently an important environmental parameter for deep-sea life. Recent biochemical studies indicated differences in protein structure and enzyme kinetics between shallow- and deep-sea animals (HOCHACHKA 1975). The structural modulations and pressure sensitivity of enzymes have come about as a consequence of speciation in the course of evolution of deep-sea animals. In my opinion, the groups and species of animals that contained the right enzyme structure and the consequent physiological adaptive strategy for high-pressure conditions are those that successfully evolved and speciated in the deep sea.

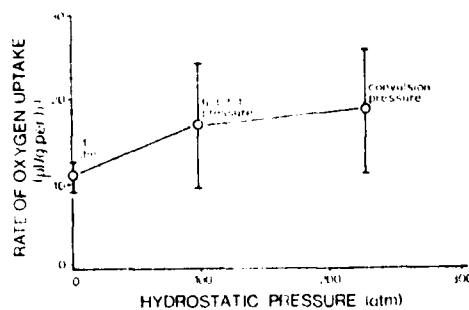


Fig. 3. Metabolic rate of the upper abyssal decapod *Parapagurus pilosimanus* in relation to pressure at 6°C.

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Appendix 3

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BEHAVIORAL AND METABOLIC ADAPTATIONS OF POLAR
AND DEEP-SEA CRUSTACEANS: A HYPOTHESIS
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EVOLUTION OF COLD ADAPTED
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BEHAVIORAL AND METABOLIC ADAPTATIONS OF POLAR AND
DEEP-SEA CRUSTACEANS: A HYPOTHESIS CONCERNING
PHYSIOLOGICAL BASIS FOR EVOLUTION OF
COLD ADAPTED CRUSTACEANS

Robert Y. George

Abstract.—This paper deals with physiological responses and behavioral patterns of cold-adapted crustaceans from the Antarctic and Arctic regions and abyssal depths. Extreme stenothermy of the abyssal amphipod *Eurythenes gryllus* and the Antarctic isopod *Glyptonotus antarcticus*, in contrast to eurythermy of the Arctic isopod *Saduria entomon*, reveals different strategies of metabolic adaptation. The low metabolic rate of a deep-living brachyuran crab *Geryon quinquidens* is compared with the fluctuating metabolic rate of an intertidal crab. Metabolic adaptations of vertically migrating crustaceans are discussed, with particular emphasis on the compensation of stimulation induced by increased pressure in reduced temperature and the oxygen minimum layer. Behavioral and respiratory responses of a eurybathic hermit crab *Parapagurus pilosimanus* from slope depths provide new data to support a hypothesis concerning adaptation to demands imposed by cold and hyperbaric conditions of the deep sea; hermits from slope depths adapted to intertidal pressures react as intertidal crabs when returned to hyperbaric conditions. The impact of past climatic conditions on thermal tolerance or sensitivity of cold adapted crustaceans is discussed with reference to evolutionary implications. Endemic Antarctic crustaceans adapted to cold-stenothermal conditions almost 30 million years before development of the Arctic cold fauna of today, hence are phenotypically less adaptive to temperature. Aside from adaptation to cold, the deep-sea fauna has added an adaptation to high pressure which is thought to be a Late Cenozoic event.

ПОВЕДЕНЧЕСКИЕ И МЕТАБОЛИЧЕСКИЕ ПРИСПОСОБЛЕНИЯ
ПОЛЯРНЫХ И ГЛУБОКОВОДНЫХ РАКООБРАЗНЫХ:
ГИПОТЕЗА, ОТНОСЯЩАЯСЯ К ФИЗИОЛОГИЧЕСКОЙ ОСНОВЕ
ДЛЯ ЭВОЛЮЦИИ ПРИСПОСОБЛЕННЫХ К ХОЛОДУ РАКООБРАЗНЫХ

Реферат.—Данная работа касается физиологических реакций и поведенческих образцов приспособленных к холоду ракообразных из Антарктического и Арктического районов и абиссальных глубин. Чрезмерная стенотермность абиссального бокоплава *Eurythenes gryllus* и антарктического равноногого рака *Glyptonotus antarcticus*, по сравнению с эвритермностью арктического равноногого рака *Saduria entomon*, указывает на различные способы метаболического приспособления. Низкая метаболическая норма глубоководного короткохвостого рака *Geryon quinquidens* сравнивается с неустойчивой метаболической нормой рака из межприливо-отливной полосы. Рассматриваются метаболические приспособления вертикально мигрирующих ракообразных, с особым вниманием на компенсацию сти-

муляции, побужденной увеличенным давлением в слоях сниженной температуры и минимального кислорода. Поведенческие и дыхательные реакции эврибатического рака-отшельника *Parapagurus isopodiformis* из глубин склона предоставляют новые данные для гипотезы, относящейся к приспособлению к требованиям холода и сверхбарометрических условий глубокого моря; раки-отшельники из глубин склона, которые приспособлены к давлениям межприливо-отливной полосы реагируют как и раки из межприливо-отливной полосы, когда возвращаются в сверхбарометрические условия. Ссылаясь на эволюционное значение, обсуждается влияние прошлых климатических условий на термальную толерантность или чувствительность приспособленных к холоду ракообразных. Эндемические антарктические ракообразные приспособились к холодно-стенотермальным условиям почти 30 миллионов лет до развития современной арктической холодной фауны, поэтому, они фенотипически менее приспособляемые к температуре. Кроме приспособления к холоду, глубоководная фауна также приспособляется к высокому давлению; это считается позднекайнозойским явлением.

Introduction

From an evolutionary viewpoint, crustaceans represent a very successful group of invertebrates that show strikingly wide adaptive radiation in the aquatic environment, as insects do in the terrestrial regime. The question here is whether the proliferation of Crustacea in the ocean is a result of behavioral patterns, metabolic adaptations, or a genetic repertoire that is a product of evolutionary adaptations. The answer to this question is undoubtedly not a simple one but there is evidence to document major adaptive strategies among crustaceans on the basis of their patterns of distribution and their physiological responses to a variety of environmental parameters such as temperature, salinity, oxygen content and hydrostatic pressure. A significant amount of physiological knowledge concerning crustaceans is already available, primarily because they are attractive and suitable animals for experimental research under laboratory conditions.

The most successful crustacean group, the Malacostraca, includes two dominant superorders: (1) the Peracarida, containing mysids, cumaceans, tanaids, isopods and amphipods; (2) the Eucarida, containing euphausiids and decapods (shrimps, lobsters, crayfish and crabs). In the tropical marine environment both eucarids and peracarids are diverse and well distributed. However, in the polar and deep-sea zones peracarids are far more successful and speciose than decapod crustaceans which appear to be impoverished in the cold southern oceans (Maxwell 1977). The Antarctic Ocean is inhabited by a diverse array of cold-adapted peracarids and the deep-sea is successfully colonized by cold- and pressure-adapted peracarids. The behavioral and metabolic adaptations of polar and deep-sea peracarid crustaceans and a slope decapod species to the stresses of low temperature and high pressure constitute the theme of this paper. An effort is made to bring out the evo-

lutionary significance of temperature and pressure adaptations in the process of speciation in the cold polar and hyperbaric deep-sea environments.

From a physiological point of view, cold adaptation entails: (1) extending the lower temperature tolerance with concomitant lowering of metabolism for energy conservation (resistance adaptations); (2) genetic establishment of cold stenothermy involving evolutionary development of genes coding for new enzyme variants to cope with low temperature with high levels of metabolism and growth (capacity adaptations); (3) structural changes in macromolecular constituents of the cell and consequent alteration in cell function; and (4) suitable biochemical changes in enzyme kinetics under high pressure and low temperature conditions that confront life processes in the deep ocean. It is now well established that pressure induces physiological trauma involving a sequence of stressful reactions such as hyperactivity syndrome (30–80 atm), convulsive episodes (80–200 atm) and paralysis (250 atm) in shallow water crustaceans (George and Marum 1974). The adaptive strategies that promote immigration and speciation in high pressure deep-sea conditions were recently discussed by George (1979a). In this paper, the temperature sensitivity of Arctic, Antarctic and abyssal crustacean species is discussed with emphasis on behavioral and metabolic responses. A hypothesis is postulated to explain the thermal physiology of cold-adapted poikilotherms as it relates to the impact of the past climatic environment.

Thermal Sensitivity of Abyssal Amphipod *Eurythenes gryllus* vs. Antarctic Isopod *Glyptonotus antarcticus*

The temperature of both the polar and the deep sea is generally less than 4°C, and, therefore, the poikilothermic crustaceans inhabiting this water are usually cold-stenothermal. The average abyssal temperature is 2°C but the hypopsychral thermal regime around the Antarctic continent is characterized by near freezing temperature (–1.8°C). In the course of evolution, Antarctic poikilotherms have developed glycoprotein antifreezes in their body fluids and blood to avoid supercooling problems during frequent contacts with ice. According to DeVries (1977), these glycoproteins are simple compounds that contain two amino acids, threonine and alanine, and the sugars, galactose and galactosamine. Deep-sea animals do not experience near-freezing temperature; in fact, in the Mediterranean the abyssal temperature is high (>16°C), and in vicinity of hydrothermal vents, as in the "hot spring" zones in the abyss close to the Galapagos Islands, deep-sea animals encounter unique conditions of high pressure and temperature. The thermal sensitivity and metabolic adaptations of these abyssal animals remain unexplored.

In a recent study, George (1977) compared the thermal tolerance of the



Fig. 1. A. Abyssal amphipod, *Eurythenes gryllus* (5 to 7 cm), captured from 2010 m in the central Arctic Ocean. B. Antarctic endemic isopod, *Glyptonotus antarcticus* (11–12 cm), photographed at 10 m in the McMurdo Sound, near Ross Island, Antarctica. Note the gigantic body dimensions of these cold-adapted crustaceans.

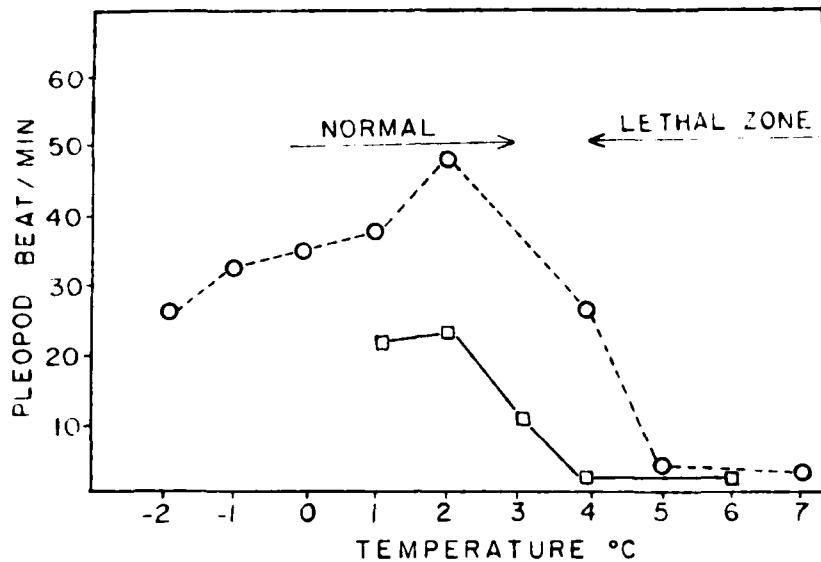


Fig. 2. Resting pleopod beat frequency in relation to temperature in the Antarctic crustacean, *Glyptonotus antarcticus* (○), and the abyssal crustacean, *Eurythenes gryllus* (□). Each data point represents a mean of 10 observations.

Antarctic isopod *Glyptonotus antarcticus* with that of the Arctic isopod *Saduria entomon*. The Antarctic isopod was found to be stenothermal in extreme cold, with the upper lethal temperature at 3°C. McWhinnie (1964) pointed out that the Antarctic krill *Euphausia superba* also has a narrow physiological temperature range with upper lethal limit around 4°C. These endemic Antarctic crustaceans with narrow thermal tolerance occur south of the Antarctic convergence in a circumpolar zone around the Antarctic continent. In contrast to the thermal sensitivity of Antarctic crustaceans, the temperature acclimation experiments of George (1977) demonstrated the eurythermal nature of the Arctic endemic isopod and amphipod crustaceans.

The thermal sensitivity of deep-sea crustaceans has not been critically evaluated thus far. Recently it has been possible to capture the scavenger type deep-sea amphipods in large numbers with the use of baited traps in the abyss (George 1979a, b; Yayanos 1978). George (1979a) used to advantage the isothermal water column of the Arctic Ocean to bring up live abyssal amphipods from the deep ocean without any apparent thermal injury. Yayanos (1978) used a trap device with pressure-temperature conservation features and brought up lysianasid amphipods alive.

The data on behavioral and metabolic responses of the deep-sea amphipod *Eurythenes gryllus* (Fig. 1) from 2010 m suggest that these abyssal crusta-

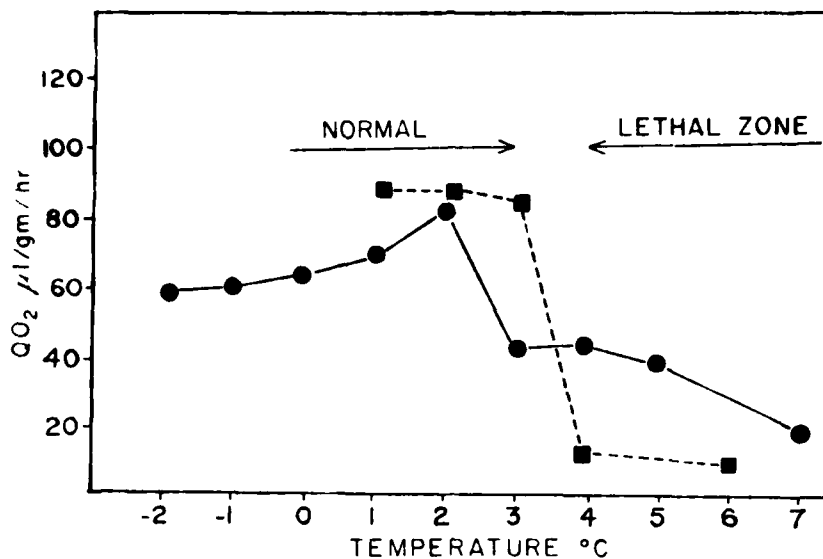


Fig. 3. Resting metabolic rate in relation to temperature in the Antarctic crustacean, *Glyptonotus antarcticus* (■), and the abyssal crustacean, *Eurythenes gryllus* (●). Each data point represents a mean of 10 measurements.

ceans have an upper lethal temperature comparable to that of the Antarctic stenothermal crustaceans (Figs. 2 and 3). The average resting pleopod beat frequency was drastically reduced at 4°C (Fig. 2). The metabolic rate also showed an abrupt 8-fold decrease at 4°C. The results of this study suggested that both species, one Antarctic and the other abyssal, are genetically adapted to cope with only low temperature conditions, unlike the Arctic crustaceans (George 1977).

Metabolic Pattern of the Intertidal Brachyuran Crab *Callinectes sapidus* vs. Slope Brachyuran Crab *Geryon quinquedens*

It is well established that crustaceans living in the intertidal and littoral zones exhibit persistent tidal and diurnal rhythms of locomotor activity and oxygen consumption in tune with the periodic tidal inundations. However, locomotor and respiratory responses of deep sea crustaceans have not been investigated over 24-hr cycles under *in situ* or laboratory conditions. In a series of experiments, the intertidal/littoral blue crab *Callinectes sapidus* and the deep-sea red crab *Geryon quinquedens* were studied at their habitat temperature over 24-hr periods to determine resting metabolic rate at frequent intervals. The results shown in Figs. 4 and 5 represent typical re-

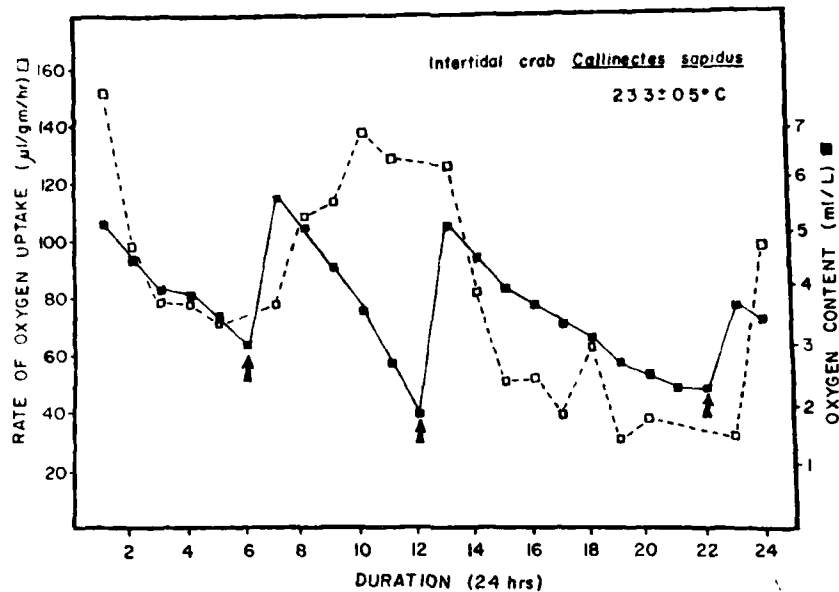


Fig. 4. Metabolic rate of the intertidal crab *Callinectes sapidus* over a period of 24 hr. Since oxygen uptake of the crab was not influenced by oxygen content less than 2 ml/L., oxygenation of the experimental chamber was made at points indicated by the arrow to maintain oxygen level above 2 ml/L.

sponse patterns in these crabs from the intertidal/littoral zone and the slope depths (850 m), respectively. The data suggest that significant fluctuations in metabolic rate characterize the response patterns of the intertidal crab. On the contrary, the deep-sea crab showed low and constant metabolic rate throughout the 24-hr period at 7°C.

In general, deep-sea crabs remain lethargic, with very little locomotor activity. Such behavior is also exhibited by temperate crabs when acclimated gradually to low winter temperatures. Reduced locomotor activity under low temperature conditions is of adaptive advantage because of the economic implications in conserving energy. Indisputably, the lethargic crustaceans in the deep depths have a metabolic rate much lower than their shallower living counterparts or congeneric species.

Metabolic Responses of Vertically Migrating Crustaceans

It is important to take into account the influence of increasing pressure on the metabolic rate of mid-water or deep scattering layer crustaceans. Pressure enhances metabolic rate of shallow water amphipods up to 140 atm

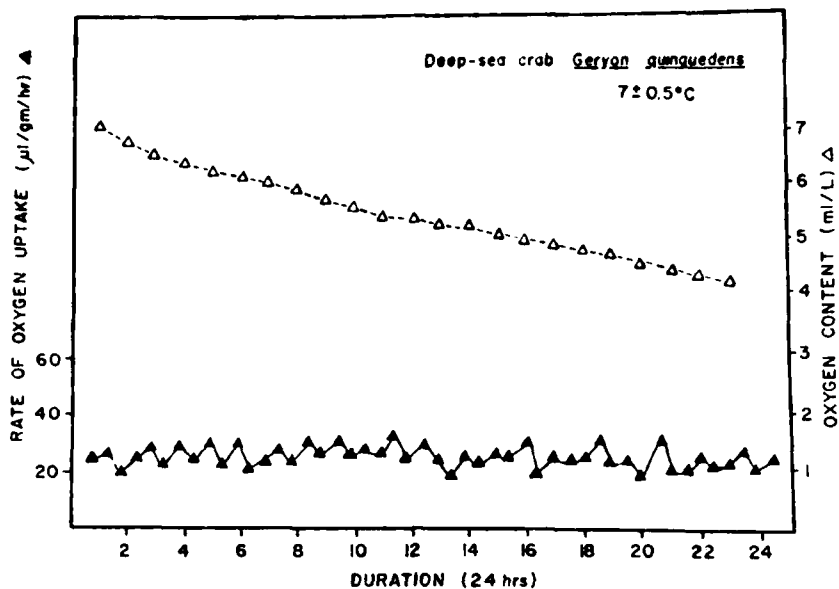


Fig. 5. Metabolic rate of the slope red crab *Geryon quinquedens* over a period of 24 hr.

and then shows inhibitory effects on metabolic rate (George 1979a). In the case of vertically migrating euphausiids Teal and Carey (1967) showed that these crustaceans lowered their metabolism at night depths (200–400 m) by occupying the oxygen minimum zone to counteract the stimulatory effect of moderate pressure (20–40 atm). Such metabolic adaptation is also seen in the deep living mysid *Gnathophausia ingens* while inhabiting the oxygen minimum layer (Childress 1968). The diurnal mid-water vertical migrator *Gaussia princeps*, a copepod that spends the day below 400 m in the oxygen minimum layer and night at about 200 m, displays a very low metabolic rate at all temperature and pressure combinations (Childress 1977). The low rate at greater depth is of special physiological implication for partially anaerobic survival in the oxygen minimum layer and is of significance due to the energy conservation role in such behavior. In open ocean temperate seas and oceanic regions lacking an oxygen minimum zone in deeper depths, the metabolic rate of vertical migrators appears to be regulated at a constant level due to the counteracting influence of decreasing temperature and increasing pressure, somewhat as depicted in Fig. 6.

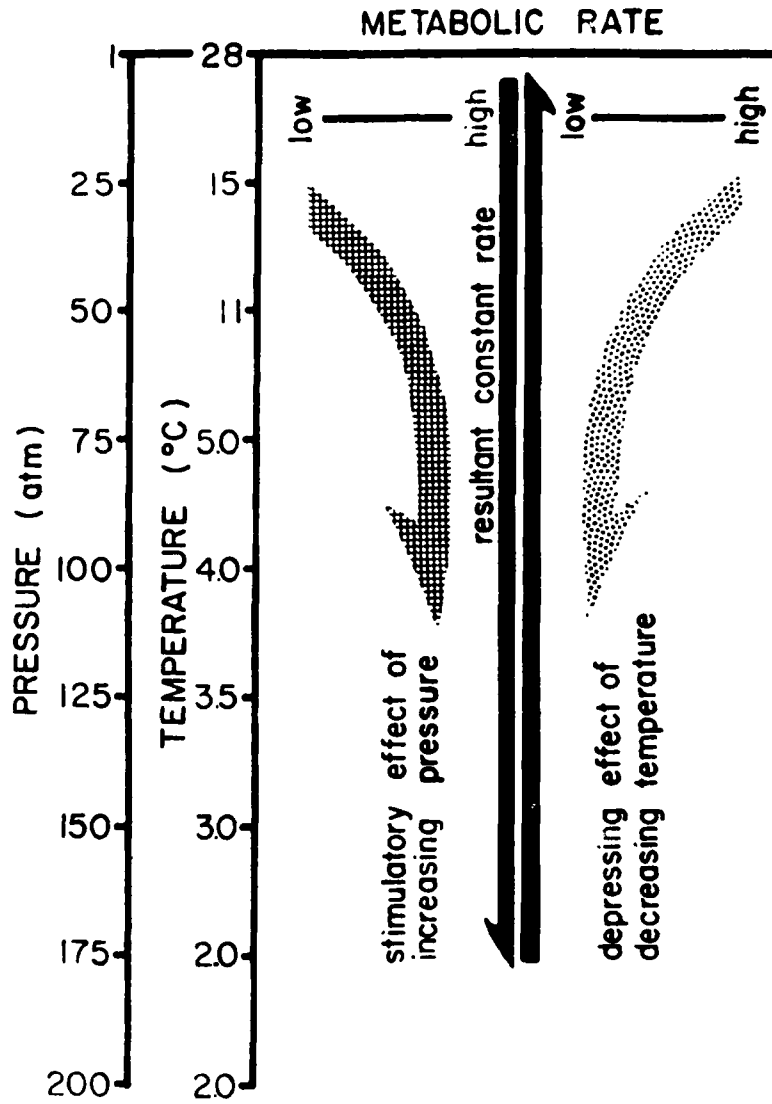


Fig. 6. A schematic representation of a model showing metabolic regulation in vertical migrators due to the interaction of pressure and temperature.

Metabolic Responses of the Slope Pagurid Crab
Parapagurus pilosimanus to Different Temperature

In a recent study on the slope hermit crab *P. pilosimanus* (George and Lilyquist 1979), it was found that deep living populations at 800 and 1600 m showed markedly different pressure responses. Crabs that were captured at 800 m convulsed at 220 ± 5 atm when recompressed in the high pressure aquarium. Crabs from 1600 m convulsed at a much higher pressure (340 ± 5 atm). However, the convulsion threshold was significantly altered during prolonged acclimation at 1 atm. After a period of 20 months at 1 atm, the deep living crabs responded as shallow water pagurid crabs, with a mean convulsion threshold at 110 atm. This finding suggests that the pressure resistance of deep living crabs from different depths is a phenotypical environmental adaptation that fades during prolonged acclimation at 1 atm.

Temperature tolerance and metabolic responses of this deep-sea crab are also noteworthy. Its optimum temperature of inhabitancy, in accordance with the definition of Golikov and Scarlato (1973), is 6°C, which is also the temperature at 800 m over the continental slope off North Carolina where peak abundance of this eurybathyal decapod species is encountered and where spawning takes place. In the laboratory it was possible to acclimate these crabs gradually (1°C increase per day) up to 16°C. In Fig. 7, the metabolic rate of this deep-sea crab, when acclimated at different temperatures, is illustrated. The data suggest that Q_{10} values are significantly attenuated in the lower temperature range and markedly elevated at higher temperature range beyond 10°C. The low Q_{10} values below 10°C are of physiological significance and indicate successful acclimation. At 16°C, the crabs showed obvious increase in locomotor activities with concomitant increase in oxygen consumption rates. Food consumption at 16°C was also considerably enhanced. However, larvae of these deep-sea crabs were found to be more sensitive to high temperature and to show great mortality above 10°C. The larval stage thus is obviously the most sensitive phase of ontogenesis, and is confined to a narrow range of temperature as dictated by the genotype. But the eurythermal nature of the adult slope pagurid crabs may be explained by the hypothesis that the adults are recent invaders into the deeper depths of the slope. Perhaps their thermal tolerance reflects the origin of this species from a temperate warm water progenitor.

A New Hypothesis Concerning Physiological Basis for
Evolution of Cold Adapted Crustaceans

It is important to point out that over the course of geologic time variations in marine climates occurred in the global marine environment. Although bipolar glacial marine climate existed in the Precambrian age, there is evidence for warm conditions in the Cambrian Antarctic and Arctic (Schwarz-

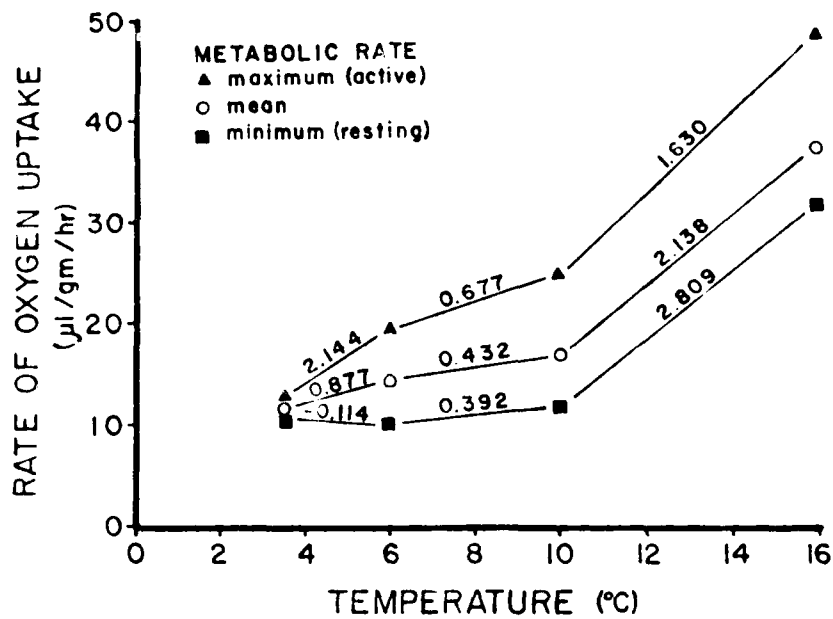


Fig. 7. Metabolic responses of the deep sea hermit crab *Parapagurus pilosimanus* to different acclimation temperatures (Data from George and Lilyquist 1979). Numerals appearing on lines connecting points represent values of Q_{10} .

back 1961). While the northern hemisphere was warm, the south polar region has undergone glaciation, according to King (1961). This situation implies that the warm adapted fauna of the southern ocean either became extinct or gradually evolved into cold adapted species. According to Schwarzbach (1961), climate was tropical throughout the World Ocean, and latitudinal stratification of temperature must have been minimal during the late Jurassic period (120 million years ago). Nevertheless, cooling of marine climate began during the Cretaceous (84–100 million years ago) when the Arctic showed a coldest temperature of 15°C (Lowenstam and Epstein 1959) and Antarctica exhibited temperate conditions (King 1961). Antarctica experienced glaciation during the post-Cretaceous period; the water temperature there gradually decreased to about 3°C in the Miocene and has remained cold at negative Celsius temperatures since the Pliocene (>13 million years). On the contrary, the Arctic Miocene temperature remained at about 16°C (Craig 1961) and continued to remain warm in the Pliocene period. The Arctic Ocean temperature reached its present polar condition (>0°C) less than 2 million years ago with the commencement of an Arctic

polar ice cap as a Pleistocene event. The above discussion indicates that the Antarctic marine fauna of today originated and attained equilibrium with cold conditions almost 30 million years earlier than the Arctic cold marine fauna. This explains why cold stenothermy is strongly implanted within the genotype of endemic Antarctic crustaceans, while wide thermal tolerance in Arctic crustaceans is suggestive of residual phenotypical plasticity.

Palaeotemperature data on Tertiary deep ocean bottom temperatures are based upon the ratio of the isotopes oxygen 18 to oxygen 16 in the calcium carbonate of fossil shells (Emiliani and Edwards 1953). The work of Emiliani (1961) on oxygen isotope measurements of benthic foraminiferans from the Pacific equatorial deep sea shows that the deep-sea temperature gradually decreased from $+14^{\circ}\text{C}$ in the Upper Cretaceous to $\pm 10.4^{\circ}\text{C}$ in the Middle Oligocene (35 million years) and further down to the present $+2.2^{\circ}\text{C}$ in late Pliocene (10 million years). This information provides the basis for the hypothesis that the Tertiary warm deep-sea fauna was killed by the marked temperature decline (Bruun 1956) and, therefore, colonization and speciation in the cold deep-sea are Late Cenozoic events (≈ 30 million years).

Against this background, if colonization of the cold polar and deep sea is examined, it becomes apparent that significant adaptive shifts must have come about in the course of speciation to cope with conditions of low temperature, as in the polar seas, and also high pressure, as in the abyss. In conformity with the views of Golikov (1973), the process of speciation in an altered environment, such as evolved during drastic temperature decline in the polar and deep sea through the geologic periods, involved as the first stage non-genetic adaptive changes in secondary and tertiary protein structure with accompanying changes in enzymes and cell metabolism. If secondary and tertiary protein structures are altered in the course of speciation, primary protein structures, as determined by the genetic code of the specific synthesis of DNA-RNA proteins, will change and become species-specific. The data presented in this paper show evidence of phenotypical changes in the species of slope decapod invading greater depths of increasing pressure. If these deep-sea invaders are able to reproduce at the greater depths and become reproductively isolated from their parental species at shallower depths of the slope, the adaptive and functional phenotypical changes may eventually become genetic adaptations to cope with low temperature and high pressure conditions of the deep sea. Biochemists offer simple hypotheses concerning evolution of the unique protein structure of deep-sea animals (Somero and Hotchachka 1976) on the basis of experimental results of depolymerization of higher orders of protein by moderate and high pressure into subunits of dimers and monomers of low molecular weight. Does this mean that deep-sea forms possess proteins that are structurally different from those of congeneric shallow species? These provocative views open new directions for research seeking answers to interesting questions involv-

ing the fundamental differences in the protein structure between shallow and deep-sea animals. Obviously more research into these intriguing questions is called for before an unequivocal interpretation is made on the biochemical and physiological implications of low temperature and pressure adaptations.

Acknowledgment

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SCIENCE

Oxygen and Carbon Isotopic Growth Record in a Reef Coral from the Florida Keys and a Deep-Sea Coral from Blake Plateau

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Oxygen and Carbon Isotopic Growth Record in a Reef Coral from the Florida Keys and a Deep-Sea Coral from Blake Plateau

Abstract. Carbon and oxygen isotope analysis through a 30-year (1944 to 1974) growth of *Montastrea annularis* from Hen and Chickens Reef (Florida Keys) shows a strong yearly variation in the abundances of both carbon-13 and oxygen-18 and a broad inverse relationship between the two isotopes. Normal annual dense bands are formed during the summer and are characterized by heavy carbon and light oxygen. "Stress bands" are formed during particularly severe winters and are characterized by heavy carbon and heavy oxygen. The isotopic effect of Zooxanthellae metabolism dominates the temperature effect on the oxygen-18/oxygen-16 ratio. The isotopic results on the deep-sea solitary coral *Bathypsammia tintinnabulum*, where Zooxanthellae are nonexistent, indicates that the abundance of the heavy isotopes carbon-13 and oxygen-18 is inversely related to the growth rate, with both carbon and oxygen approaching equilibrium values with increasing skeletal age.

The possible relationship of incremental banding in corals to environmental conditions was first investigated by Ma (1) and later by Wells (2) and Scrutton and Hipkin (3). The annual character of banding in *Montastrea annularis* has been established by both radiochemical methods (4) and direct field observations (5).

Weber and Woodhead (6, 7) showed that although hermatypic corals deposit their carbonate material in disequilibrium with seawater, the slope of the curve showing the relationship between oxygen isotopic composition and ambient temperature is the same as that given by the equation of Epstein *et al.* (8). These authors maintained that after a suitable, constant correction is applied, oxygen isotopic data from hermatypic corals can be used for paleoclimatological studies. Land *et al.* (9), however, showed that different parts of the same coral colony, and even different parts of the same corallite, may give different oxygen isotopic compositions. They found that faster-growing sites within a colony were further out of isotopic equilibrium than slower growing sites.

Weber and Woodhead (6) and Goreau (10) developed models to explain the oxygen and carbon isotopic composition of reef-building corals. According to the quantitative model developed by Goreau (10, 11) for carbon, skeletal carbon is derived from the organism's internal inorganic carbon pool, the isotopic composition of which is determined by the input of seawater HCO_3^- and respired metabolic CO_2 and by the output of excreted inorganic carbon and carbon fixed photosynthetically by symbiotic Zooxanthellae. It is expected that the carbon and oxygen isotopic composition of the skeletal parts will vary depending on the isotopic composition of the various contributors and sinks and their relative magnitudes. Because metabolic carbon is some 13 to 17 per mil lighter and meta-

bolic oxygen some 10 per mil lighter than seawater carbon and oxygen (in HCO_3^-), the skeletons of reef-building corals are lighter in both carbon and oxygen isotopic composition. Rates of growth of skeletal elements and changes in Zooxanthellae activity also affect the isotopic

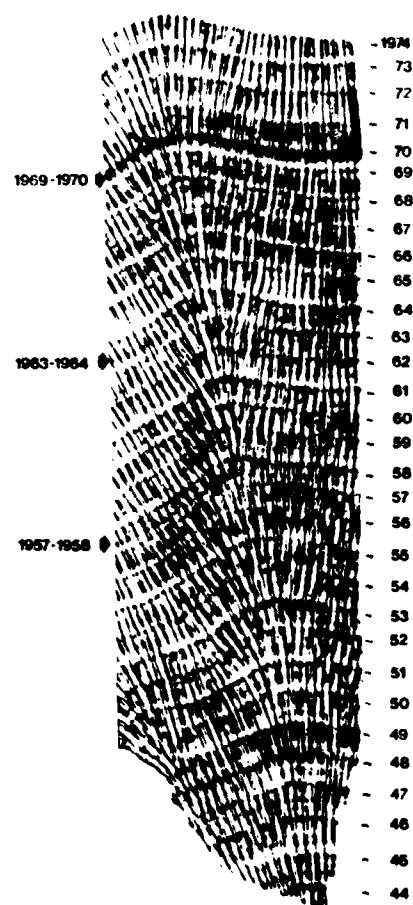


Fig. 1. X-radiograph of the section of *Montastrea annularis* analyzed isotopically. The numbers at the right indicate the year of deposition of the regular dense bands (months of August and September in each case). The numbers at the left identify abnormal dense bands deposited during particularly cold winters.

composition. [Faster-growing corallites are isotopically lighter, and greater Zooxanthellae activity will increase the production of both lighter metabolic carbon and heavier seawater carbon (6, 9, 10).] These various parameters, variously operating in different environments and at different times of the year, complicate the simple relationship between oxygen isotopic composition and temperature observed by Weber and Woodhead (7).

Annual skeletal growth in *M. annularis* consists of a thin, dense layer followed by a thicker, less dense layer. The denser layer appears to be produced by a temporary thickening of dissepiment structures and closer bundling of sclerodermites. Although hermatypic corals are known to grow throughout the year, the obvious layering of *M. annularis* suggests the possibility of different growth rates during the year. Hudson *et al.* (5) and Goreau (11) published x-radiographs of slabs cut from colonies of *M. annularis* from, respectively, Hen and Chickens Reef in the Florida Keys (24°56'N, 80°33'W) and Discovery Bay in Jamaica. In the Jamaican specimens the dense layers appear to have been formed in November and December, if one assumes constant growth (11, figure 1a). On the other hand, direct field observation of the Hen and Chickens Reef specimens clearly demonstrates that the yearly dense layers were formed during the months of August and September (5, figure 2). The lowest temperature of the year occurs at both locations during January and February (11, figure 3). In either case, therefore, it appears that the dense layers are formed before the winter temperature minimum.

A portion of a coral head of *M. annularis* from a depth of 3.6 m at Hen and Chickens Reef, representing growth from 1944 to 1974 (Fig. 1), was analyzed for carbon and oxygen isotopes. About four samples were obtained from each yearly growth, using a small grinding wheel. The results (Fig. 2) show a very strong yearly variation in both isotopes. In almost all cases the dense layers have a high ^{13}C concentration and a low ^{18}O concentration. However, in most cases, the extremes in these two parameters were reached after the dense layers were deposited—that is, in the winter. There is a broad inverse correlation between ^{13}C and ^{18}O (Fig. 3), which is not in agreement with previous observations showing little (11, figure 3) or no (7, figures 1 to 3) correlation.

The enrichment in ^{13}C observed in the dense layers may have resulted from a temporary reduction in Zooxanthellae activity, requiring more seawater carbon

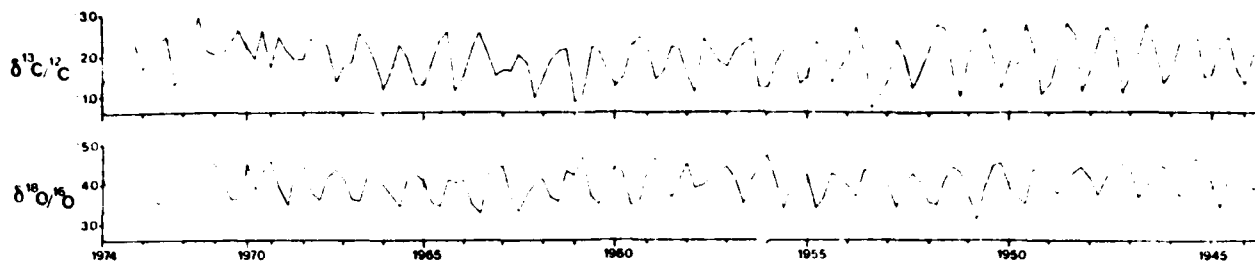


Fig. 2. $\delta^{13}\text{C}/^{12}\text{C}$ and $\delta^{18}\text{O}/^{16}\text{O}$ (per mil, with respect to the Chicago standard PDB-1) for the period 1944 to 1974, obtained from the section of *M. annularis* illustrated in Fig. 1. Divisions on the abscissa refer to the months of August-September of each year.

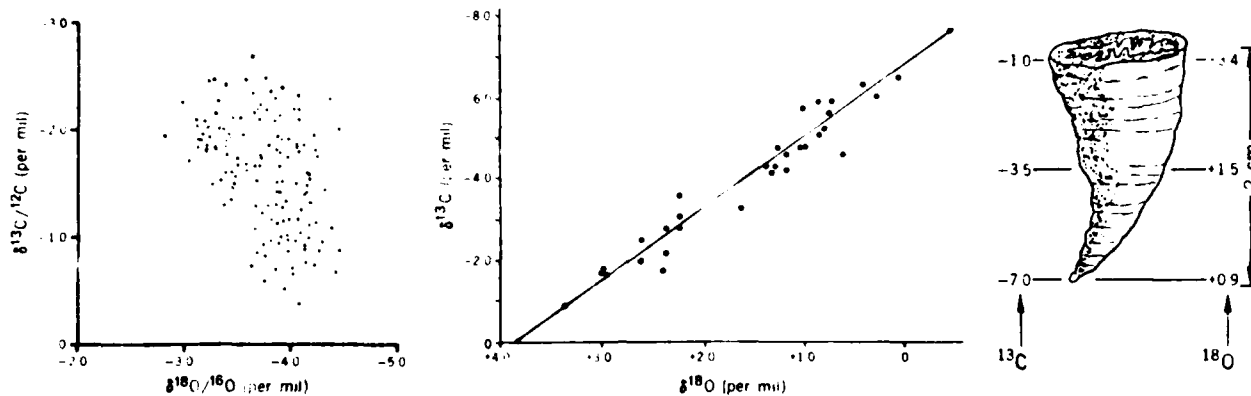


Fig. 3 (left). Relationship between carbon and oxygen isotopic composition in the time series illustrated in Fig. 2. Fig. 4 (middle). *Bathypsammia tintinnabulum* from the Blake Plateau escarpment: relationship between carbon and oxygen isotopic composition of samples taken along growth lines at different intervals from the base (upper right) to the top (lower left) of the calyxes of different adult specimens. Fig. 5 (right). *Bathypsammia tintinnabulum* from the Blake Plateau escarpment showing isotopic change during growth.

to enter the skeleton and increased deposition of sclerodermites (thereby producing the dense layers themselves) to eliminate the carbon normally removed by the Zooxanthellae. The ensuing slower growth would also favor the concentration of ^{13}C in the skeleton (9). The oxygen isotopic composition is affected not only by various physiological parameters mentioned but also by the ambient temperature. Thus, the ^{18}O depletion in the dense layers is undoubtedly in part due to the higher temperature at which these layers were formed. Three-year water temperature averages at Hen and Chickens Reef ranges from 20.9°C (January) to 29.4°C (July), which corresponds to a change of 2.1 per mil in the equilibrium oxygen isotopic composition. As shown in Fig. 2, the isotopic range is only about 1 per mil. It is apparent, therefore, that the temperature effect is masked by oxygen isotopic changes caused by variations in physiological activity.

Hudson *et al.* (5) find a correlation between some wide, high-density bands and severe environmental stress. More particularly, they consider that these bands (called stress bands to distinguish them from the normal yearly dense bands) were formed during the especially cold winters of 1941 to 1942, 1957 to

1958, 1963 to 1964, and 1969 to 1970. Of these unusually cold winters, those of 1957 to 1958 and 1969 to 1970 were the most severe (5, figure 3). Figure 2 shows that at these times the regular periodicity of the curve is broken, suggesting interruption of growth.

In ahermatypic corals living below the euphotic zone, Zooxanthellae are missing and the relationship between oxygen and carbon isotopes is much clearer. Weber (12) demonstrated that deep-sea ahermatypic corals are generally less depleted in ^{13}C and ^{18}O than hermatypic corals. We have analyzed incrementally several skeletons of the solitary coral *Bathypsammia tintinnabulum*, collected from a depth of 850 m on the Blake Plateau escarpment (32°33'N, 76°59'W), where Zooxanthellae do not exist and the yearly temperature range is small (4.5° to 6.0°C). This deep-sea solitary coral, whose skeleton seldom exceeds 2.5 cm in height, exhibits regular and irregular growth rings. These epithecal rings may represent a longer growth period and a greater amplitude than those of *M. annularis*. Although the yearly temperature range is negligible or nonexistent in the dark and seasonless deep water, it is possible that endogenous physiological rhythms may govern the growth patterns. We can only conclude

on the basis of the isotopic data that the growth rate in this deep-sea solitary coral decreases from the base up, reaching zero when maturity is attained. The isotopic results (Fig. 4) reflect the growth pattern, with both carbon and oxygen approaching equilibrium values with increasing skeletal age (Fig. 5). Ahermatypic corals of this type can therefore be used for paleotemperature studies.

It is apparent from this study that strong yearly isotopic variations occur in the growth of the reef coral *M. annularis* (Fig. 2). These variations are deeply affected by the presence of Zooxanthellae, as indicated by previous studies (6, 7, 9-11). It appears that much work remains to be done before an unequivocal interpretation of the carbon and oxygen isotopic results is obtained in terms of basic environmental parameters.

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Eutrophic hadal benthic community in the Puerto Rico Trench

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Abstract

The hadal benthos of the Puerto Rico Trench suggests that a eutrophic system is present in two areas where an abundance of plant debris and other organic material are introduced into a suitably oxygenated bottom water mass. This is evidenced by a standing crop of meiofauna, 91 to 97% nematodes and harpacticoid copepods, between 17059 and 17303 individuals/m², based on two box corer samples taken at 8560 and 8580 m in the Brownson Deep. Analysis of two otter trawl samples of macrofauna revealed the presence of a wide spectrum of species representing different trophic types. Osmotrophic organisms such as actinarian anthozoans and pogonophorans and wood-infesting caudofoverate gastropods are common in the eutrophic Gilliss Deep. Deposit feeding animals such as holothurians, isopods, amphipods and cumaceans represent the dominant trophic type, at 7600 m in the Gilliss Deep and 8800 m in the Brownson Deep. The use of the Puerto Rico Trench as a site for waste disposal is questioned on the basis of the eutrophic character and the relatively unpredictable tectonic nature of the trench.

Introduction

The use of the ocean floor as a vast receptacle for waste disposal has become a common practice in recent years and has resulted in the introduction of continually increasing quantities of both inert and toxic materials into the sea. This economically popular activity has generated considerable concern over the consequences of this method of disposal, especially when the disposal sites are in relatively shallow coastal zones along the continental shelf. Baseline investigations have also been conducted in some of the designated deep sea dumping sites to identify possible contamination and to study the effect of disposal on the marine biota (1, 2). Ocean trenches have been proposed as potential sites for waste disposal since they, unlike other deep-water sites, offer an alleged isolation of the materials dumped. Unfortunately, we know very little about these unique areas of the sea.

Trenches, of which there are about 22 throughout the world, are generally located in the vicinity of the continental margins or island arcs and therefore this geographic setting adjacent to land masses enhances a natural dumping of terrestrial and coastal material, both inorganic and organic. The trenches are characterized usually by steep walls and a flat plain at the bottom. The depth of trenches ranges from 4000 to nearly 11 000 m, thereby including both abyssal (3000–6000 m) and hadal (>6000 m) faunal zones. Life associated with the trench floor, particularly at hadal depths, is uniquely adapted to cope with extreme hydrostatic pressure and special trophic

conditions (3, 4, 5) and it is a reasonable assumption that such life is in a very delicate balance with its environment.

The Puerto Rico Trench embraces the greatest known depths of the Atlantic Ocean and represents the only hadal zone in the Northwestern Atlantic Ocean. This continuous linear depression of the sea floor extends nearly 1000 km from East to West between 50 and 100 km North of Puerto Rico and the Leeward Islands of the Lesser Antilles (Fig 1, 2). The Puerto Rico Trench floor at hadal depths is wider (35–55 km) than the floor of other trenches (5–12 km). The northern boundary of this trench is formed by scarps and a complex ridge system. A steep wall constitutes the southern boundary (Fig 3). Geological investigations of the trench have given us a relatively comprehensive understanding of its topography (6). However, we know very little about the benthic communities on the trench floor and scheduled dumping of waste materials in the Puerto Rico Trench is imminent. This paper focuses upon the structure of the hadal benthic community of two selected areas located within the Puerto Rico Trench.

Previous studies of the Puerto Rico Trench

The emphasis on previous studies in this subtropical Atlantic trench has been on geological and geophysical aspects which were largely initiated during the establishment of the "mohole" project which involved deep drilling along the northern ridge of the trench. Geologists who investigated this trench concluded that it resulted from tension between the Caribbean and American tectonic plates instead of originating from compression and down-buckling (6). The rectangular cross-section of the trench suggests that a fissure, filled by subcrustal upwelling or by turbidity current-transported sediment, also contributed to the formation of the flat trench floor.

The sedimentation pattern in the Puerto Rico Trench has been the subject of a recent study (7). Thick beds of homogenous silty clay make up most of the graded beds in the deepest basins of the trench floor. Topographic variations and sedimentary properties suggest that the bottom layers were deposited by turbidity currents originating from the shelf adjacent to Puerto Rico and the Leeward Islands of the Lesser Antilles, and flowing through numerous canyons northward into the trench plain where they spread laterally. This same sedimentation study reports that the turbidity current is powerful enough to deposit 20 to 50 cm of fine sand as far away as 100 km from the point of entry into the trench floor. The enhanced turbidity flow over the trench wall is the possible cause of considerable erosion as evidenced by the occurrence of numerous rock outcrops and older Miocene sediments along the trench wall. The abyssal plain sands of the trench are mainly composed of a heterogeneous



Fig 1. The Puerto Rico Trench showing the extent of the hadal zone below 6000 m depth, and the three "deeps" discussed in this study.

mixture of calcareous and terrigenous detritus. The analysis of the upper 10 m of the trench floor sediment suggests that these sediments have been deposited during the Pleistocene. The sediment in the Brownson Deep region of the trench primarily consists of shallow deposits interbedded with typical deep sea red clay and occasional Miocene lutite. In the western parts of the trench, within the Milwaukee Deep, an anoxic sediment regime has been encountered (8). The proximity of the Mona Canyon (Fig 2) to the western area of the trench also serves as a major source of deposition of shallow sediment and thereby promotes organic enrichment of the trench.

An earlier study on the water of the Brownson Deep (9) found that the water mass below the sill is somewhat homogeneous. This study also concluded that the source of the deep water adjacent to the trench floor is essentially modified antarctic bottom water (ABW) from the South Atlantic (Fig 3). This deep water flow enters the trench from the East and flows over the trench bottom in a westward direction. The circulation within the trench basin is undoubtedly influenced by the ridge system but the pattern of water flow is poorly understood. Perhaps the anoxic conditions in the western portion of the trench is



Fig 2. The Brownson and Gilliss Deeps of the Puerto Rico Trench showing the study sites and transect (A-F) corresponding to the trench, shown in Fig 3.

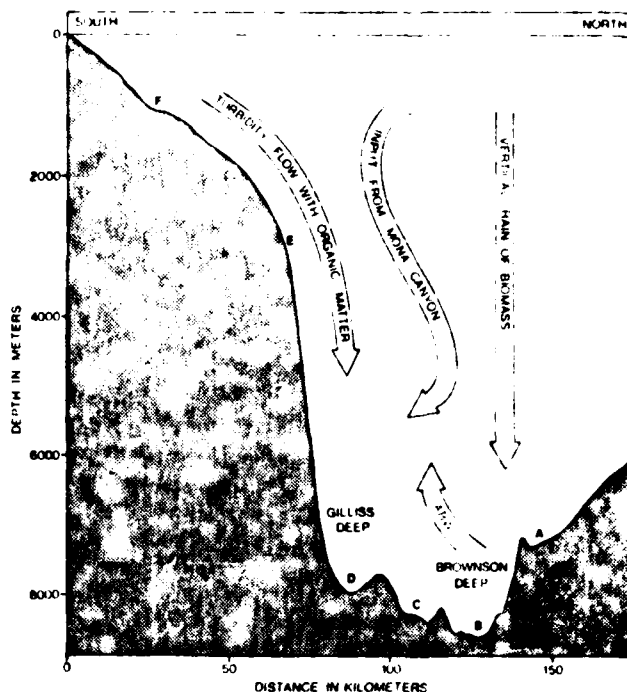


Fig 3. Vertical profile of the Puerto Rico Trench based on a precision depth recorder trace along the transect (A-F) shown in Fig 2. Position "A" is the site of the "Mohole". Note the steep wall along the southern edge of the trench and the ridges on the trench floor that may serve as dams between the Gilliss and Brownson Deeps. Sources of organic transport to the trench floor are indicated by the arrows. "ABW" indicates Antarctic Bottom Water.

attributable to a feeble mixing process. The accumulated organic matter in the anoxic region was probably converted by bacterial activity into low molecular substances like methane and hydrogen sulfide. The spatial and temporal limits of this anoxic region of the Puerto Rico Trench is unknown.

Biological studies of the Puerto Rico Trench have been few. The first effort to study the trench was the Johnson-Smithsonian Deep-Sea Expedition of the early 1930's. Although this effort was unsuccessful in obtaining samples from the trench floor some trawl samples were obtained from the trench wall (10). The first biological samples from the trench floor (7000 m) were obtained during the Swedish *Albatross* Cruise in 1948. Material from this effort included specimens of foraminifera, holothurians, large amphipods and fishes (11). The Danish *Galathea* Expedition in the early 1950's investigated two stations in the trench, at 1240 and 2840 m.

In 1964, the French deep-diving bathyscaphe, *Archimede*, explored the Puerto Rico Trench through ten dives to depths of 9000 m (12). The observations along the southern side of the trench confirmed the existence of a decantation process which contributes to an increase in the deposition of organic material over the trench floor. Two special dives were devoted to biological observations. These two dives, particularly the dive to 7300 m, revealed the presence of a benthic hadal fauna consisting of "fair numbers" of a holothurian (*Myrrochus*), a decapod crustacean (*Nematocarcinus*), a giant isopod crustacean (probably *Storhyngura*), and large numbers of a liparid fish (*Careproctus*). The hadal brotulid fish, *Bassogigas profundismus*, was collected from the Puerto Rico Trench floor in a 1969 cruise by Pillsbury (13). Some additional information on the hadal faunas was provided from trawl

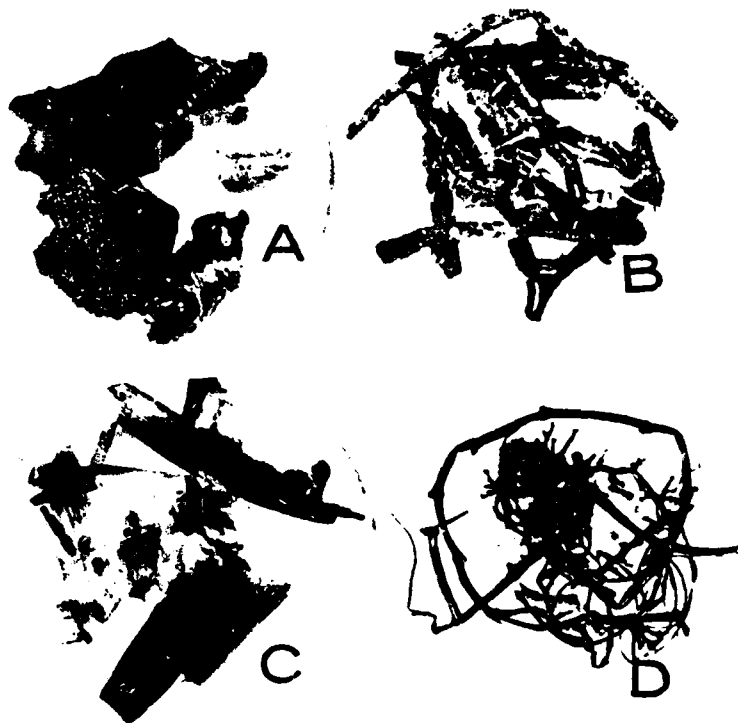


Fig. 4. Samples of human refuse and plant debris from the Gilliss Deep (7200 m) taken by the otter trawl. A. Pieces of rope; B. *Thalassia* rhizomes; C. Eel grass blades; D. Red algae (*Grassolaria follifera*).

samples taken during the 1973 cruise of the Soviet *Akademik Kurchatov* (14).

Recent studies: The R/V Gilliss Cruises

During the summers of 1976 and 1977 we conducted a benthic sampling program aboard the R/V *Gilliss* to study the hadal community of two sites within the Puerto Rico Trench. These sites were selected on the basis of a preliminary study of the trench topography between longitude 66 and 68° W (Fig 3). The northern study site was located in the central portion of the relatively flat Brownson Deep (19.8 to 20.0° N, 60 to 64° W) at 8860 m. The southern study site, which we propose be named the *Gilliss Deep*, constitutes a well-defined basin at depths between 6000 and 8000 m; the samples which we will discuss currently were taken at a depth of 7200 m.

The Brownson Deep and the Gilliss Deep are separated by a ridge system which begins at a depth of 6200 m on the floor of the Mona Canyon (to the Southwest) and extends eastward. The topographic features of the trench probably have a significant influence on the trophodynamics of the hadal benthic community. The Brownson and Gilliss Deeps appear to receive different magnitudes of organic inputs from the Mona Canyon whose physiography acts like a funnel for the plant-derived organics originating from the nearby land masses. The Milwaukee Deep, West of the Mona Canyon, also receives large quantities of organic material but probably lacks the oxygenation to assimilate this input.

Hadal benthic animals were collected by two methods.

A 40-ft otter trawl fitted with a 500 μm -mesh cod end was used for sample periods of 4 hours duration at a speed of 1.5 knots over a distance of about 7–11 km along an east-west axis (Fig 3). These samples were sorted immediately upon retrieval to separate the various types of plant material and benthic fauna. The wet weight of the fauna was determined by use of a Mettler analytical balance. The macrofaunal constituents (those larger than 500 μm) were identified to the lowest taxonomic level possible. Seven such trawl samples were taken although the data from only two samples are described in this report.

Five quantitative benthic samples were taken from the Brownson Deep between 8500 and 8600 m. The results of two of these samples are the basis for the following discussions. A box corer, capable of taking an undisturbed sample with a surface area of 0.03 m² (17.0 × 19.5 cm), was fitted with screened vents and flapper valves to reduce the bow-wave effect. A pinger was placed 50 m above the box corer in order to accurately monitor its distance from the trench floor. The corer was lowered at a rate of 100 m/min until it reached a depth 50 m above the floor and was then eased slowly into contact with the sediment. Two subsamples, with a surface area of 25 cm² (2.5 × 10 cm) and a depth of 7 cm, were taken from each box corer sample. Each subsample was sliced horizontally into 1 cm strata down to 7 cm. These subsamples and the remaining portions of the box corer samples were processed separately through 500 μm and 62 μm mesh sieves. The organisms were preserved in formalin and later counted and identified to major taxon. Specimens have subsequently been sent to specialists for species identification.



Fig 5. Samples of wood from the Gilliss Deep (7200 m). A. Holes (about 1 mm diameter) and grooves indicating possible borer activity; B. *Storhyngura*, a hadal giant isopod. It is still uncertain whether or not the wood-infesting deep-sea isopods utilize wood for food.

Trawl samples – rich in plant debris

Each of the seven trawl samples, two from the Gilliss Deep (7200 m) and five from the Brownson Deep (8600 m) contained a surprising abundance of plant material and human refuse that included corroded cans, bottles, a dinner plate and cup, bits of rope, cigarette butts and pieces of cardboard (Fig 4A). The plant debris, however, was more biologically significant and included a diverse array of coconut husks, sugarcane, bamboo, broken branches and twigs of trees, seeds, eel grass (*Zostera marina*), turtle grass rhizomes and blades (*Thalassia*) and the seaweed *Sargassum* and a red alga (*Grassolaria*) (Fig 4). The biomass of plant material ranged from 1.5 to 8.5 kg per trawl sample. Such plant material has been shown to be significant in the ecology of the hadal benthos (15, 16). There were, in general, greater quantities of plant materials found in the samples taken from the Gilliss Deep than from the Brownson Deep. It seems likely that the location of the Gilliss Deep at the base of the nearly vertical trench wall on the southern, landward side of the trench may account for the apparent greater accumulation of plant material in this area. Much of this material is the result of regional tropical storms. Another source of transport of plant material into the trench basins is the turbidity flow from the Mona Canyon.

In an oligotrophic (low nutrient) deep-sea benthic environment such as we find in the central abyssal plains and trenches isolated from land masses, organic matter which serves as food for the benthic fauna consists essentially of insoluble, macromolecular and residual substances. In contrast, the rich input of plant material received by an adequately oxygenated trench basin such as those under discussion, promotes a more eutrophic (high nutrient) condition. This is reflected in the composition and number of benthic fauna of a given area. Another indication of the eutrophic character of the Brownson and Gilliss Deeps is the relatively low redox potential of the sediment (+40 to -30 mv). Furthermore, the sediment of these two deeps contains relatively high amounts of organic carbon (1.5% of dry weight). The amount of dissolved organic carbon in a hadal water sample taken about 25 m above the trench floor (0.8 mg/l) was similar to the amounts recorded for more shallow abyssal regions (0.7-0.9 mg/l) (17).

Wood Infesting Organisms

The samples of wood from the trawl showed obvious signs of biodeterioration – many grooves and holes (Fig 5A). Insect and crustacean borers are more commonly found in shallower environments, with the exception of the



Fig 6. Wood-infesting cocculinid gastropods from the Puerto Rico Trench. A. Typical specimen from the Gilliss Deep; B. Specimen located in one end of a depression in the wood. Scale is in mm.

molluscan borer, *Xylophaga*, which is found in the upper abyssal zones near continental slopes (18). Wood from the trench floor did not contain the true marine borers such as shipworms (*Teredo*, a mollusc) and gribbles (*Limnoria*, a flabelliferan isopod crustacean). However, asellote isopods, including the genera *Ischnomesus* and *Heteromesus*, along with cocculinid gastropods (Fig 6) were found in the various crevices and grooves in the wood. The probable use of plant material for shelter and food by abyssal isopods has been suggested in a previous report (15). It is still not known whether or not these hadal wood-infesting organisms are equipped with a cellulolytic enzyme or with gut-bacterial populations which digest wood.

Hadal macrofauna of different trophic types

The hadal zone is characterized by organisms with unique biological properties (3). We know that eutrophic trenches in the vicinity of land are associated with terrigenous

material. Oligotrophic trenches are generally far from land and under surface waters of low productivity. The present study suggests that within the Puerto Rico Trench, a variety of ecological conditions may be present primarily as a result of the topographic configurations.

Osmotrophic Organisms: A comparison of major trophic types, based on the macrofauna encountered in the two trench basins (Table 1) suggests that pogonophorans and actinarians are commonly found in the Gilliss Deep. Barophyllic bacteria from this trench show heterotrophic activity by uptake of dissolved organic carbon from the ambient environment (19). Pogonophorans that lack a well-defined alimentary tract, are well-known examples of osmotrophic nutrition because of their ability to absorb dissolved organic carbon through the body wall (20). Our samples from the Gilliss Deep contained many pogonophorans and the endemic hadal anemone, *Galathea-themum* (Fig 7). These animals are indicator osmotrophic organisms which appear to characterize eutrophic trench zones.



Fig. 7. Typical vermiform macrofauna from the eutrophic Gilliss Deep. A. Echiurids; B. Sipunculids; C. Tube-dwelling actinarian anthozoans (*Galathea themus*).

Table 1. Macrofauna: Abundance, biomass and trophic types in the Puerto Rico Trench.

Trophic Type and Taxon	Gilliss Deep, Station 24 (7600 m)		Brownson Deep, Station 20 (8800 m)	
	Number of Indi- viduals	Biomass in gms	Number of Indi- viduals	Biomass in gms
Osmotrophic				
Anthozoa: Actinaria	64	162.40		
Pogonophora	62	3.84		
Detritophagous				
Sipunculida	2	2.84		
Priapulida	2	0.86		
Echiurida	8	4.08		
Polychaeta	17	2.96	8	1.04
Nemertina	1	1.08		
Porifera	2	0.28		
Gastropoda: Cocculinidae (wood-infesting)	16	0.06	4	0.02
Crustacea: Isopoda	18	1.06	12	1.22
Crustacea: Tanaidacea	1	0.40	4	0.06
Echiurida	8	4.08		
Polychaeta	17	2.96	8	1.04
Nemertina	1	1.08		
Detritophagous				
Porifera	2	0.28		
Gastropoda: Cocculinidae	16	0.06	4	0.02
Crustacea: Isopoda	18	1.06	12	1.22
Crustacea: Tanaidacea	1	0.40	4	0.06
Crustacea: Cumacea			4	0.10
Holothuroidea (<i>Elpidia</i>)	18	8.10	4	2.20
Pices (<i>Cars proctus</i>)	1	2.80		
Detritophagous-Carnivorous				
Amphipoda			6	0.88
Carnivorous				
Pices (<i>Gomostoma</i> & <i>Photostomias</i>)	14	142.60	6	32.40
Crustacea: Decapoda (<i>Plesio- penus</i> & <i>Nematocarcinus</i>)	8	296.00		
Pelecypoda: Septibranchia	4	2.14	1	0.52
Crustacea: Ostracoda			8	0.02
Total Animal Biomass	238	631	57	38.46
Total Plant Biomass		75		742.00

Detritophagous Organisms: The most dominant trophic type encountered both in the Gilliss and Brownson Deeps, evidently is a detritophagous mode of feeding (Table 1). Vermiform organisms such as sipunculids, priapulids, echiuroids, polychaetes and nemertines are particularly conspicuous in the samples from Gilliss Deep. Other detritophagous or deposit feeding animals include the holothurians, fishes and crustaceans (Isopods, Tanaids and Cumaceans). A new species of the isopod genus *Storhyngura* was found to occur commonly in the Puerto Rico Trench basins (Fig 5B). This genus appears to exhibit the phenomenon of abyssal giantism, and the hadal species from this trench is 28–32 mm in comparison with the average size (2–3 mm) of other abyssal asellote isopods. Furthermore, it is of interest to note that the genus *Storhyngura* is distributed primarily in Antarctic waters and hadal regions of other trenches (21). It is likely that the presence of this animal in the Puerto Rico Trench has been influenced by the flow of Antarctic bottom water (ABW) entering from the East.

Carnivorous Organisms: The bottom samples from the Puerto Rico Trench contained both benthic and benthopelagic fishes belonging to the genera *Gomostoma* and *Photostomias*. These fishes possess enlarged mouths to capture large prey organisms. The scavenger type lysianassid amphipods and natantian decapods are also found to occur in the hadal depths of the Puerto Rico Trench. In both Brownson and Gilliss Deeps, septibranch pelecypods were collected. The molluscs are well-known examples for carnivorous mode of feeding.

Hadal meiofauna

As a matter of convenience in sample processing, sediment is passed through a series of sieves which include a 1.0 mm mesh sieve to retain macrofauna and a 62 μm (or 40 μm) mesh sieve which retains a size-defined assemblage of metazoan and protozoan (mostly foraminiferans) invertebrates. Our knowledge of deep-sea meiofauna is limited to only a few papers (22). One study has included material from 6036 m, a sample from the abyssal plain in the Central North Pacific (23). A second study by the same investigators, includes hadal material from the Aleutian Trench at a depth of 7200 m (24). Both studies utilized a box corer in the sampling procedure. In the present study, the meiofaunal community has been examined on the basis of two box corer samples from 8560 m in the Brownson Deep, the deepest known site from which meiofauna has been collected.

Two major taxa of invertebrates, nematodes and harpacticoid copepods, dominated (91–97%) the meiofauna community in the Brownson Deep (Table 2). The standing crop of meiofauna was 17059 individuals/m² at Station 07 and 17307 individuals/m² at Station 09. Abundance data were calculated on the total sorting of each box corer sample to a depth of 7 cm. These figures are much lower than the 210111 individuals/m² recorded from abyssal depths of 5250 to 5750 m in the Iberian Sea (22); however, the meiofaunal densities from the hadal zone of the Puerto Rico Trench are much larger than the 2152 individuals/m² recorded from the single hadal sample from the Aleutian Trench.

Although the Aleutian Trench sample was taken with a box corer, the abundance datum is unfortunately based on the use of a 297 μm mesh sieve instead of a 62 μm mesh sieve which is more standard for meiofaunal analyses. One sample from the North Pacific study was sieved with both 297 μm mesh and 150 μm mesh sieves; a total of 260 individuals/m² was calculated from the material retained by the 297 μm mesh sieve and 800 individuals/m² in the case of the 150 μm mesh sieve (22). Another sample, "washed by a 62 μm mesh sieve yielded an order of magnitude greater abundance of meiofaunal taxa" (25). Using this as a basis for extrapolation, if the 2152 individuals/m² datum for meiofaunal abundance in the 0–8 cm stratum of the Aleutian Trench sample is increased by "an order of magnitude", the meiofaunal densities of the Brownson Deep and Aleutian Trench may be roughly equivalent.

Although there appears to be some similarity in the

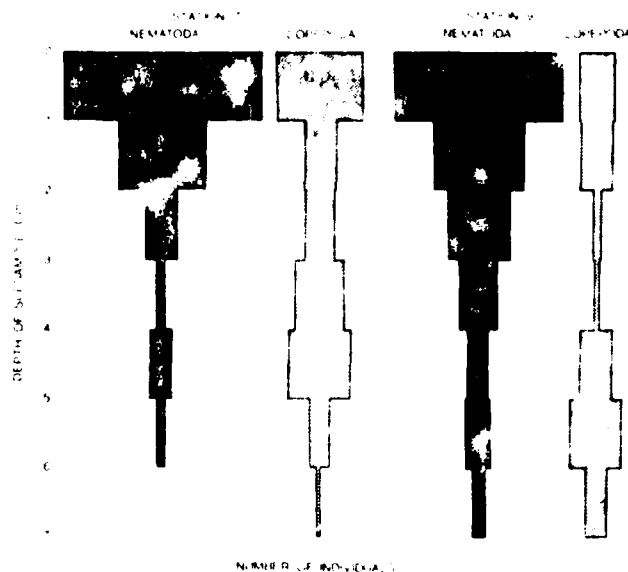


Fig. 8. Vertical distribution of the dominant meiofauna, nematodes and harpacticoid copepods, in subsamples of sediment from two box corer samples from the Brownson Deep.

standing crop between the Aleutian and Puerto Rico Trenches, the faunal composition differs. The large numbers of allogromiid foraminifera found in the Aleutian sample are not present in the Puerto Rico Trench samples. Foraminifera were not counted in our study during the sorting process but it was obvious that they were of little numerical significance.

The vertical distribution of meiofauna in each box corer sample was determined by slicing each meiotic corer subsample into 1 cm strata from the surface to 7 cm. The analysis of the results of sieving each stratum is shown in Fig 8. Nematodes are dominant in the upper strata while the harpacticoid copepods dominate the lower strata.

The Puerto Rico Trench as a disposal site

In recent discussions on the concept of deep-sea dumping, trenches were considered as a potential site for the disposal of high level nuclear wastes (26). The principal reason for rejecting the uses of trenches for dumping is the proximity of these sites to human populations. Furthermore, unlike the oligotrophic midgyre regions, trenches are close to biologically productive oceanic and neretic zones and hence the problem of effluents entering the marine food chain and ultimately becoming incorporated into the human diet. In addition, the tectonically active nature of the trench environment introduces an unknown but potentially hazardous risk.

Anoxic trench basins may offer environmental attributes more acceptable for deep-sea dumping. The Cariaco Trench along the coast of Venezuela is the world's largest known tropical anoxic basin. Some areas of the Puerto Rico Trench also are anoxic or hypoxic; however, we know very little about the potential for a change in circulation patterns which could alter these zones and allow entrapped effluents to invade adjacent biologically productive areas. Low species diversity, relatively low biomass, and an apparently low metabolic activity alone may not offer valid biological criteria for management decisions relevant to the use of trench floor environments

Table 2. Meiofauna: Abundance in the Puerto Rico Trench.

Taxon	Brownson Deep, Station 07 (8560 m)		Brownson Deep, Station 09 (8580 m)	
	Number Individuals/m ²	Percent of Total	Number Individuals/m ²	Percent of Total
Nematoda	11 022	65	13 901	80
Copepoda: Harpacticoida	4 520	26	3 003	17
Amphipoda	31	< 1	31	< 1
Isopoda			31	< 1
Pelecypoda	31	< 1	31	< 1
Gastropoda	279	2	31	< 1
Unidentified (soft bodied)	1 176	7	310	2
Total (Standing Crop)	17 059		17 307	

for waste disposal. Deep-sea disposal sites are chosen evidently on the basis of several criteria other than biological constraints.

Within the Puerto Rico Trench there exists a designated deep-water dump site which should be carefully studied not only from the standpoint of what fauna exists and what biological processes and food chains prevail, but also from the standpoint of the potential interactions between this site and the adjacent regions. The present study indicates that there is an abundance of osmotrophic organisms in the hadal benthos. These animals are trophically adapted to utilize the dissolved organic matter in the ambient water. The hadal benthos include benthopelagic amphipods and fishes that scavenge upon corpses of animals on the trench floor and further serve as nutrient sources which enter more shallow water zones. Thus, the energy flow and flux within the hadal food chain deserve careful analysis.

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