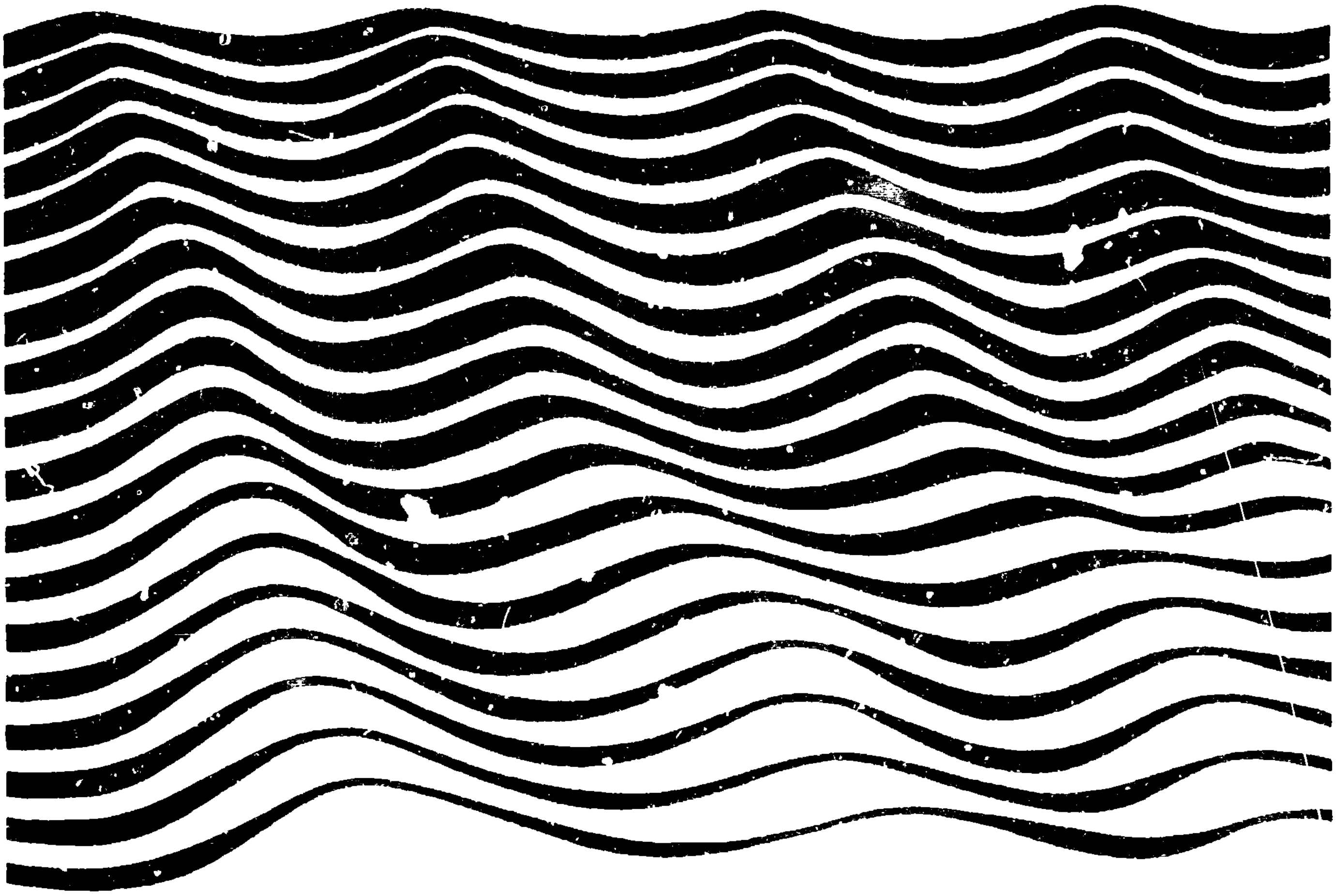
Unesco technical papers
in marine science 49

Pelagic biogeography

Proceedings of an
international conference
The Netherlands
29 May-5 June 1985



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41	Ocean-Atmosphere Materials exchange (OAMEX) Report of SCOR Working Group 44, Unesco, Paris, 14-16 November 1979	1982	WG 44
42	Carbon dioxide sub-group of the joint panel on oceanographic tables and standards. Report of a meeting Miami, Florida, 21-23 September 1981 sponsored by Unesco, ICES, SCOR, IAPSO	1983	—
43	International Symposium on Coastal lagoons Bordeaux, France, 8-14 September 1981 Available in F and S	1982	—
44	Algorithms for computation of fundamental properties of seawater. Endorsed by Unesco/SCOR/ICES/IAPSO Joint Panel on Oceanographic Tables and Standards and SCOR Working Group 51.	1983	—
45	The International System of Units (SI) in Oceanography Report of IAPSO Working Group on Symbols, Units and Nomenclature in Physical Oceanography. (SUN)	1985	—
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Edited by:
A.C. Pierrot-Bults
S. van der Spoel
B.J. Zahuranec
R.K. Johnson

ICoPB
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PREFACE

This series, the Unesco Technical Papers in Marine Science, is produced by the Unesco Division of Marine Sciences as a means of informing the scientific community of recent advances in oceanographic research and on recommended research programmes and methods.

The texts in this series are prepared in co-operation with non-governmental scientific organizations. Many of the texts result from research activities of the Scientific Committee on Oceanic Research (SCOR) and are submitted to Unesco for printing following final approval by SCOR of the relevant working group report.

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ABSTRACT

The International Conference on Pelagic Biogeography (ICoPB) was held at Noordwijkerhout, Netherlands, from 29 May to 6 June 1985.

The conference was scheduled around nine topics in a combined symposium/workshop format. It brought together active workers on phytoplankton, zooplankton, fishes, cetaceans, scientists from a variety of disciplines, ecologists, systematists, historical biogeographers, palaeontologists and physical oceanographers.

The conference recognized a.o. the need:

1. To incorporate modern concepts and theory on biogeography in pelagic oceanography, such as cladistics and vicariance, and to relate modern distribution patterns with patterns and changes read from the fossil record.
2. To develop adequate sampling techniques.
3. To stimulate systematic studies utilizing both traditional and recently developed approaches such as genetic/biochemical methods and studies of living organisms both in situ and in culture.
4. To carry out additional mapping studies, also advocating the use of existing collections.
5. To study the congruencies of distribution patterns and to test the hypothesis that closer correspondence between major distribution patterns and large-scale current patterns is related to marked changes in productivity.

This report does not consist of polished and finished research documents. The deliberately short papers are an outpouring of ideas, where we are now and where we ought to be going.

RESUME

La Conférence internationale sur la biogéographie pélagique (ICoPB) s'est tenue à Noordwijkerhout (Pays-Bas), du 29 mai au 6 juin 1985.

Conçue sous la forme d'un colloque/atelier, cette conférence s'articulait autour de neuf thèmes. Elle a rassemblé des chercheurs dont les travaux ont trait au phytoplancton, au zooplancton, aux poissons ou aux cétacés et des scientifiques spécialisés dans diverses disciplines (écologie, systématique, biogéographie historique, paléontologie et océanographie physique).

La Conférence a reconnu en particulier la nécessité :

1. d'intégrer dans l'océanographie pélagique la théorie et les notions modernes de la biogéographie, telles que la cladistique et la vicariance, et d'établir des relations entre les caractéristiques de la distribution actuelle et les caractéristiques et évolution que l'on peut déduire de l'étude des fossiles ;
2. de mettre au point des techniques d'échantillonnage adéquates ;
3. d'encourager la réalisation d'études systématiques utilisant à la fois les approches traditionnelles et les approches nouvelles, telles que les méthodes génétiques/biochimiques, ainsi que l'étude des organismes vivants in situ et en culture ;
4. d'entreprendre de nouvelles études de cartographie tout en stimulant l'exploitation des collections existantes ;
5. d'étudier les concordances des caractéristiques de la distribution et de soumettre à l'épreuve des faits l'hypothèse selon laquelle l'étroite correspondance qui existe entre les grandes caractéristiques de la distribution et celles des courants est liée à des modifications marquées de la productivité.

Le présent rapport ne prétend pas rassembler des documents de recherche soigneusement rédigés et mis au point. Les communications, délibérément courtes, se bornent à énoncer des idées brutes pour tenter de faire le point sur la situation actuelle et sur les objectifs vers lesquels on devrait tendre.

RESUMEN ANALITICO

Del 29 de mayo al 6 de junio de 1985 se celebró en Noordwijkerhout (Países Bajos) la Conferencia Internacional de Biogeografía Pelágica.

En la Conferencia se examinaron nueve temas y el método de trabajo asumió las formas de un simposio-taller. Participaron en la reunión científicos dedicados a la investigación del fitoplancton, el zooplancton, los peces y cetáceos, así como especialistas de una gran variedad de disciplinas, tales como la ecología, el análisis sistémico, la biogeografía histórica, la paleontología y la oceanografía física.

La Conferencia señaló la necesidad de llevar a cabo las siguientes tareas:

1. Incorporar en la oceanografía pelágica la teoría y los conceptos biogeográficos más avanzados -como la noción de especies vicariantes- y relacionar los modelos modernos de distribución con los modelos y cambios estudiados en los fósiles.

2. Crear técnicas adecuadas de muestreo.

3. Estimular la realización de estudios sistemáticos basados tanto en los enfoques tradicionales como en los de reciente elaboración -por ejemplo, los métodos genético-bioquímicos- y de estudios relativos a los organismos biológicos in situ y en cultivo.

4. Llevar a cabo estudios cartográficos complementarios, fomentando a la vez la utilización de las colecciones cartográficas ya existentes.

5. Estudiar las congruencias de los modelos de distribución y poner a prueba la hipótesis de que la estrecha correspondencia entre los modelos principales de distribución y los modelos de las corrientes en gran escala está relacionada con cambios acentuados de la productividad.

En este informe no se recogen documentos de investigación revisados y definitivos. En cambio, se presentan textos deliberadamente breves, pero ricos en ideas, sobre el estado actual y la orientación futura que debería imprimirse a las actividades en esta esfera.

РЕЗЮМЕ

С 29 мая по 6 июня 1985 г. в Нордвикерхауте, Нидерланды, состоялась Международная конференция по пелагической биогеографии (МКПБ).

В тематику работы Конференции входили девять вопросов, которые рассматривались в рамках сочетания симпозиума и учебно-практического семинара. На Конференцию приехали специалисты, работающие в области фитопланктона, зоопланктона, рыб, китообразных, ученые по различным дисциплинам, экологи, специалисты по классификации, по исторической биогеографии, палеонтологи и специалисты по физической океанографии.

Наряду с другими вопросами Конференция признала необходимым:

1. Включить современные концепции и современную теорию биогеографии в пелагическую океанографию, как например, типологию и викарность, а также связать современные особенности распределения видов с особенностями и изменениями, полученными при классификации ископаемых.

2. Развивать соответствующие методы взятия проб.

3. Стимулировать проведение систематических исследований с использованием как традиционных, так и современных подходов, таких как генетические/биохимические методы, а также исследования живых организмов как в среде обитания, так и при искусственном выращивании.

4. Осуществить дополнительные исследования по картированию, содействуя также использованию существующих сборников.

5. Изучить соответствия особенностей распределения и проверить гипотезы о том, что близкие соответствия между основными особенностями распределения и широкомасштабными текущими особенностями связаны с отмеченными изменениями в продуктивности.

Этот доклад состоит не из отработанных и законченных исследований. Преднамеренно краткие работы представляют собой изложение идей, о существующем в настоящее время положении и перспективах развития.

خلاصة

عقد المؤتمر الدولى للجغرافيا الحيوية لمياه المحيطات ، فى نوردفيكرهوت، بهولندا من ٢٩ مايو / أيار الى ٦ يونيو / حزيران ١٩٨٥ .

وتناول المؤتمر تسعة موضوعات ، ونظم فى آن معا فى شكل ندوة / حلقة عمل ، وحضره متخصصون فى البلانكتون النباتى ، والبلانكتون الحيوانى ، والأسماك، والثدييات البحرية ، وعلماء من مختلف التخصصات ، وعلماء بيئة ، ومصنفون ، وأخصائيو جغرافيا حيوية تاريخية ، وعلماء الأحافير القديمة ، وأخصائيو أقيانوغرافيا طبيعية .

واعترف المؤتمر على الأخص بالحاجة الى ما يلى :

١ - ادراج المفاهيم الحديثة ونظرية الجغرافيا الحيوية فى مجال مياه المحيطات ، كالنظرية القائلة بانتماء مجموعة من الكائنات الى أصل واحد cladistics ، أو بالاحلال الايكولوجى والطوبولوجى فيما بين الأنواع والأجناس vicariance ، وربط أنماط التوزيع الحديثة بالأنماط والتغيرات المستنبطة من سجل الأحافير .

٢ - استنباط تقنيات ملائمة لأخذ العينات .

٣ - الحفز على اجراء دراسات منتظمة عن طريق استخدام كل من النهوج التقليدية والنهوج المستنبطة حديثا ، كالأساليب القائمة على علم الوراثة والكيمياء الحيوية ، ودراسة الكائنات الحية فى كل من مواقعها الأصلية ومواقع تربيتها .

٤ - اجراء دراسات خرائطية اضافية ، والمناداة باستخدام المجموعات المتوافرة .

٥ - دراسة نواحى تطابق أنماط التوزيع واختبار الفرضية القائلة بأن الارتباط الوثيق الموجود بين أنماط التوزيع الرئيسية أنماط التيارات ذات النطاق الواسع ، ذو صلة بالتغيرات الملحوظة فى الانتاجية .

ولا يحتوى هذا التقرير على بحوث " مصقولة " وكاملة . فالمقالات قصيرة عمدا ، وهى عبارة عن فيض من الأفكار تبين وضعنا الآن وما ينبغى أن نتوصل اليه .

摘　　要

１９８５年５月２９日至６月６日在荷兰诺德克豪特召开了国际大洋生物地理学会议（ICoPB）。会议采取一种讨论会／讲习班相结合的形式，围绕着９个专题进行。它汇集了积极从事浮游植物、浮游动物、鱼类、鲸类动物研究的工作人员，不同学科的科学家，生态学家，分类学家，历史生物地理学家，古生物学家及物理海洋学家。

会议确认必须：

１。在远洋海洋学中加进诸如遗传因素和替代性这些生物地理学方面的新概念和新理论，并把现代的分布模式与化石记录上辩认出来的模式和变化联系起来。

２．发展适当的采样技术。

３。促进同时使用传统方法和新近研制的方法（如遗传／生物化学方法）进行系统研究以及对现场的和培殖的生物有机体进行研究。

４．进行更多的测绘研究，并提倡利用现有的各种收集资料。

５。研究各种分布模式的一致性，并检验以下假说，即主要分布模式与大规模的现行模式之间的极其相似性同生产力的显著变化有关。

本报告包括的研究文件未经过推敲，很不完善，这些故意写得较短的文章只是提出一些想法，说明我们的现状及今后的方向。

FOREWORD

In early 1983 Sir Alister Hardy was informed about the plans for the International Conference on Pelagic Biogeography -ICoPB. With great enthusiasm he encouraged the organizers and accepted membership of the Comittee d'Honneur, but complained that he probably would not be able to attend; we are indeed very sorry that he could not. Not only did Sir Alister Hardy stimulate the conference, but also was near the cradle of much of the research discussed during the conference. It is therefore with pleasure that we dedicated this conference in his honour on behalf of the plenary meeting of ICoPB.

As host of ICoPB I am glad to thank also Dr. R. Revelle, Rear Admiral J. C. Kreffers, Dr. O. A. Skarlatto, Dr. T. Tokioka and Dr. K. Verhoeff for their help as members of the Comittee d'Honneur, giving the conference its broad scientific and international basis.

Thanks are expressed to our colleagues Drs. R. K. Johnson and B. J. Zahuranec for creating the initiatives for ICoPB and to Drs. T. S. S. Rao and G. R. Hasle for their stimulating work in the scientific committee. Dr. A. C. Pierrot-Bults took care of the daily organization of ICoPB and coordinated the editing of the present volume, we all are indebted for this great help.

The funding agencies: United Nations Educational, Scientific and Cultural Organization, International Association on Biological Oceanography, National Science Foundation U.S.A., Ministry of Education and Sciences of the Netherlands, the Royal Netherlands Academy of Sciences, Office of Naval Research U.S.A., Netherlands Council for Sea Research and the Amsterdam University Society are acknowledged with sincere thanks for their essential support. Their stimulating advice and cooperative attitude was noted with pleasure by the organizing committee.

September 1986
Dr. S.van der Spoel

IN MEMORIAM
Professor Sir Alister Hardy, F.R.S.

Alister Clavering Hardy was born in Nottingham, on February 10th 1896. He died on May 22nd 1985 after a long and distinguished career, first as a zoologist and marine ecologist. He was also a religious thinker and he founded The Religious Experience Research Unit, Manchester College, Oxford, where he was director, and which now bears his name (The Alister Hardy Research Unit).

After school at Oundle he went up to Exeter College, Oxford in 1914. In 1915 he volunteered for war service, eventually becoming Assistant Camouflage Officer to the 13th Army Corps in 1918. Returning to Oxford in 1919 he graduated with distinction in 1921, when he was appointed Assistant Naturalist at the Fisheries Laboratory in Lowestoft.

His research at Lowestoft, especially that concerned with food relations during the life history of the herring, supported his selection in 1924 as Chief Zoologist on the first of the Colonial Offices' "Discovery" expeditions. This was to investigate the biology and hydrography relating to the Antarctic whale fisheries. He returned in 1927 with a mass of data and new ideas, notably on vertical migrations and the exclusion of animals from dense populations of phytoplankton, and on those stimulated by his investigation of plankton patchiness through trials with his continuous plankton recorder. These ideas had to wait, for very soon after his return he was appointed as the first Professor of Zoology in the newly founded University College of Hull.

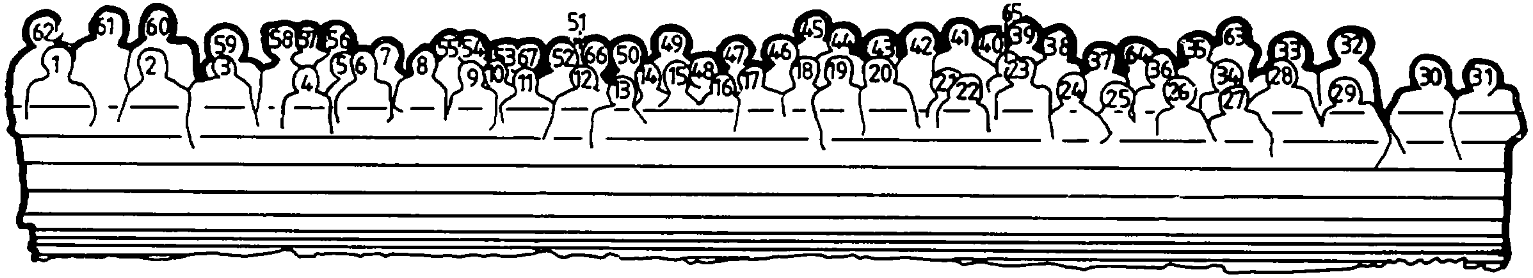
There, beside all the work involved in setting up a new department, he was planning an imaginative research project, based on an improved model of his continuous plankton recorder. This led in 1931 to the opening of a joint Department of Zoology and Oceanography at Hull. The aim of the recorder programme, and Hardy had the charm and drive to obtain the grants and colleagues to realise his plans, was to provide regular (usually monthly) charts of the distribution of plankton in the North Sea and adjacent waters. Such qualities and ingenuity were evident also in his use of kites to fly nets, which could be opened and closed like plankton nets, to sample the aerial plankton. The recorder programme was well under way and showed much promise when the war came.

In 1940 he was elected Fellow of the Royal Society, and then in 1942 he was appointed to the Regius Chair of Natural History at Aberdeen University. In 1946 he was invited by Oxford University to become Linacre Professor of Zoology. While he was at Aberdeen and Oxford, and after he retired, he continued to take a close interest in the continuous plankton recorder surveys. Actually, on his departure for Aberdeen he was made Honorary Director of Oceanographical Investigations at Hull and he was also editor-in-chief for the first six volumes of the *(Hull) Bulletins of Marine Ecology*, which was needed to publish their ever expanding records. By 1968, thirty-three merchant ships and weather ships of seven countries provided 120,000 miles of sampling with continuous plankton recorders. More than ever they appreciated that biogeography gave their studies a firm base.

During his three professorships Hardy was also involved in experimental ecology. For instance, there was his work with Neil Paton on the vertical migration of plankton animals, also cut short by the war, and his experiments with Richard Bainbridge (1951 and 1954) using their plankton wheel to measure the rate of ascent and descent of the animals. After he retired from his Linacre Chair in 1961, he became Director of Field Studies, Oxford, for two years. He was also a Fellow of Merton College, later an Honorary Fellow of Exeter College. He was knighted in 1957.

He married, in 1927, Sylvia Lucy, daughter of Professor Walter Garstang. She died soon after he did, but they leave a son and daughter. He was a friendly and courteous man, above all with a keen sense of loyality. His eagerness and enthusiasm were infectious and he was not afraid to speculate, if there seemed to be supporting evidence. Moreover, he had admirable gifts as an artist and a writer. His book *Great Waters*, which is based on his antarctic journals, gained him a Phi Beta Kappa Award for science as literature in America. His religious ideas were developed in his Gifford Lectures, which he gave in Aberdeen in 1963-65, later published as *The Living Stream* and *The Divine Flame*. The former was awarded the Lecomte de Nouy prize at Yale University. Not long before he died he learned that he had been awarded the 185,000 dollar Templeton Prize for Progress in Religion. Thus, his work as a religious investigator continues as well as the development of his scientific endeavours.

N. B. Marshall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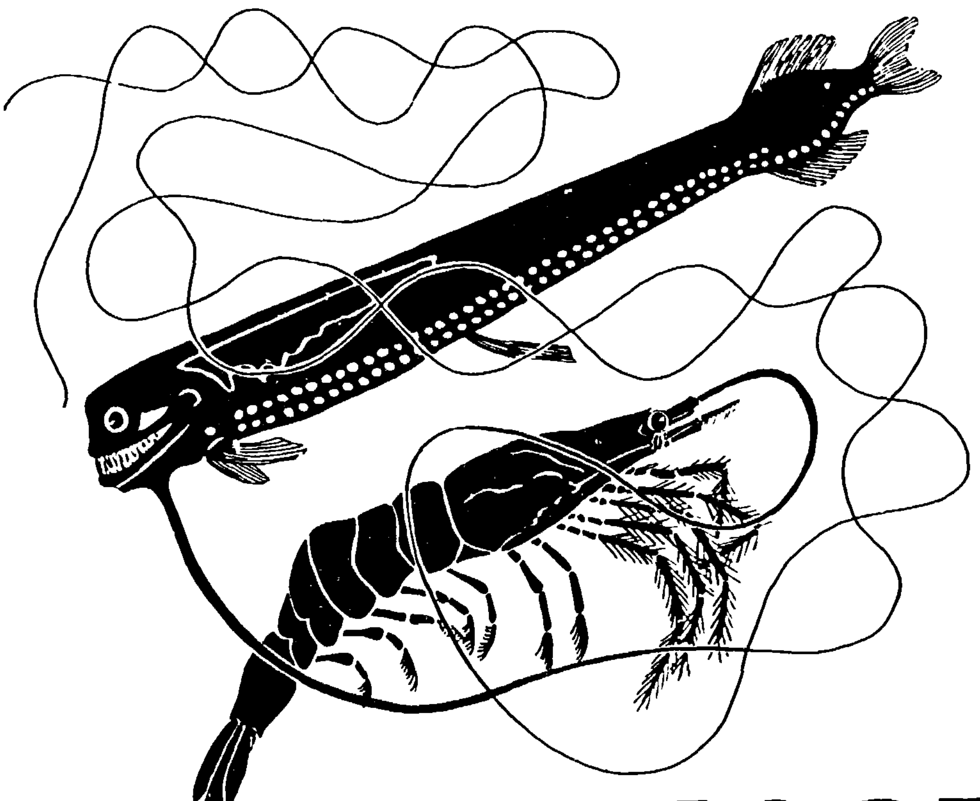
ICoPB



1985

INTRODUCTION

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"Biogeography cannot confine itself simply to describing the occurrence of living forms, arranging them regionally, investigating the ecological causes of distribution. It must also proceed historically." (Ekman, 1953).

Biogeography is commonly defined as the study of distribution of organisms on a large scale, typically on a global scale. Pelagic biogeography deals with these patterns in the pelagic realm of the world's ocean. The patterns are influenced by ecological and historical processes on many temporal and spatial scales that are only poorly understood. Thus, more inclusively, pelagic biogeography is the study of the origin, change and maintenance of patterns in the distribution of pelagic marine organisms in space and time. In this broad sense pelagic biogeography is the most synthetic field of open-ocean biology. It is also, arguably, the most diffuse, and it is in great need of advancing through testable hypotheses, rigorous concept and theory.

Taking the above into account, the "International Conference on Pelagic Biogeography" (ICoPB) in the Netherlands from 29 May - 6 June 1985 was initiated in order to address the status of the field. Eighty-five scientists from fifteen nations (Argentina, Australia, Belgium, Canada, F.R.G., France, India, Israel, Japan, Mexico, the Netherlands, Norway, U.K., U.S.A., U.S.S.R.) attended the conference or contributed to these proceedings. The participants included active open-ocean researchers embracing the broadest possible diversity of groups and approaches: ecologists, systematists, workers on phytoplankton, zooplankton, fishes and cetaceans, historical biogeographers, paleontologists, and physical oceanographers. Specialists who seldom if ever directly interact were brought together.

The conference programme was designed around nine topic areas, to be covered in turn by symposium sessions of presented papers, and in workshop discussion sections. The main subjects discussed and reflected in this volume are: uniqueness of pelagic biogeography (Brinton & Reid p.25; Hasle p.118; Johnson p.156; McGowan p.191; Van der Spoel p.254), the congruency of epi-, meso- and bathypelagic patterns and vertical distribution (p.3; Casanova p.42; Cohen p.54; Godeaux p.104; Harbison p.112; Kikuchi & Omori p.172; Loeb p.177; Merrett p.201; Parin p.226; Pugh p.230), the role of populations and patches (Haury p.126; Katona p.166; Mauchline p.186; Venrick p.261), the relevance of genetic studies (Bucklin p.35; Marcus p.182), the role of life history strategies (Caswell p.47; Cresswell p.60; Dale p.65; John p.149; Scheltema p.242), variation and the species concept (Gibbs p.98; Shih p.250 de Visser p.266), boundaries and transition zones (Backus p.9; Boltovskoy p.14; Chandramohan p.51; Domanski p.73; Olson p.219; Rao & Madhupratap p.235; Wormuth p.270), vicariance biogeography and paleoceanography (Fleminger p.84; Herman p.141; Nelson p.214 Ress p.237) and the role of regional and temporal variability in primary and secondary production (Haedrich p.107; Hayward p.133; Nair p.210; Yentsch & Garside p.278).

The organizers especially tried to stimulate the incorporation into pelagic biogeography of modern viewpoints such as: population genetics, autecology, cladistics, vicariance, plate tectonics and paleocirculation patterns and results from the deep sea drilling programme.

During the first part, the participants presented their assessment based on their own experiences and on information from the literature. Forty-five papers were presented in these symposium sessions. The participants were encouraged to make presentations that would define, address and discuss the outstanding questions of open-ocean biogeography in an attempt to determine where we are and where we ought to be going. Consequently, some of the ideas presented were controversial and speculative. This also helps account for some of the diversity of the presentations. The papers, of neccessity short, often in abbreviated form, constitute the body of this volume. Since the nine topics are more or less overlapping, the papers in this volume are presented in alphabetical order. This volume indicates the goals which may be reached with new approaches and the neccessity of special techniques, laboratory and museum facilities and management.

During the second half of the conference, all participants took part in series of workshops discussing the nine topics, which resulted in nine working group reports. These have been condensed and are edited as the Summary Report and Recommendations, General Conclusions and Specific Recommendations.

This volume compiled by selected scientists tries to mark the pathway for pelagic biogeography in the near future. During the last decade a number of publications adequately pictured the present stage of the field (Beklemishev, 1969 ; McGowan, 1972; Charnock & Deacon, 1978; Van der Spoel & Pierrot-Bults, 1979; Van der Spoel & Heyman, 1981). Discussions should now focus on the question what to do in the future. We hope some of these questions will be answered by this volume.

One of the first results of the Conference was the establishment of a non-profit foundation in the Netherlands entitled "Stichting International Conferences on Pelagic Biogeography (ICoPB)". The aims of this foundation are to:

-organize an International Conference on Pelagic Biogeography in 1990 and afterwards

-execute activities in the field of pelagic biogeography including work towards the publication of this proceedings volume.

-maintain and expand contact between interested parties and institutions in the field

-publish and distribute papers on pelagic biogeography and

-participate in activities of a possible SCOR working group.

Individuals interested in participating in the accomplishment of the aims of the foundation should contact one of the editors of this volume.

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VERTICAL DISTRIBUTION : STUDY AND IMPLICATIONS

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INTRODUCTION

The oceanic water column is characterised by vertical gradients in environmental characteristics, some of which are highly correlated, whereas others are more or less independent. The abiotic properties include a wide range of physico-chemical characteristics, some unaffected by biological processes (e.g. temperature, hydrostatic pressure, density, water column stability and solubility compensation depths), but others are influenced to some extent by biological processes (e.g. light intensity and colour balance, dissolved oxygen, nutrient and certain trace element concentrations, dissolved organic concentrations, particulate size spectra and fluxes). Many abiotic properties have a major influence on the biotic characteristics such as primary production, standing crops, turn-over rates, food availability, predation pressure, micro-organism activity, morphological and physiological adaptations, particulate production and recycling, species richness and diversity. Those biological properties which are under most direct physical control can be fairly well modelled, and hence their profiles predicted with a reasonable degree of accuracy, given an adequate physical data set, e.g. primary production (Platt, Mann & Ulanowicz, 1981). But, whereas the gross patterns can be predicted, the detailed relationships between species composition and between small scale spatial phenomena remain unresolved.

DISCUSSION

Each species is faced with a multi-dimensional matrix of gradients within which it has to find its niche. Each individual lives within a hypervolume limited by the conditions for survival which may shift during its life cycle, but in many cases there is a more restricted hypervolume within which it can successfully breed. Biogeography is the study of the integration of all the individual hypervolumes for each species's total population and its interaction with historical events. A species may not occupy the whole of its potential range because in the past it has been inhibited in its spread; for example, species endemic to the Southern Ocean may be capable of living in Arctic waters.

Every individual organism needs to achieve four basic objectives in order to be biologically successful: 1) it must breed, and hence 2) it must be able to find enough food; 3) survive in the face of predation pressure; and 4) live within its energetic resources. The optimum conditions for one objective may differ quite markedly from those for another. This lack of compatibility is evident in the water column, in which a species may find optimum feeding conditions in the near-surface layers, whereas predation pressure may be much reduced deeper down, where also the cooler water temperatures may result in metabolic processes being more efficient (Iwasa, 1983). Natural selection can be expected to have resulted in each species evolving a near unique example in the spectrum of solutions to the problem of balancing the trade-offs; competition occurring where two sympatric species have arrived at similar solutions. These solutions, in essence, underlie all autecological studies involving aspects of life-histories (e.g. ontogenetic migrations and diapause), morphological and biochemical adaptations (e.g. patterns of coloration and types of bioluminescence) and behavioural characteristics (e.g. diel vertical migrations).

Any particular species may have a critical stage in its life history at which the limits for its survival are more restricted than at others. These limits will then define the core of its distribution; the periphery of this core-range will be extended by diffusion and advection in passive species and by migrations in more mobile species.

Long-term climatic variations in water

structure may have left persistent imprints on the pattern of species distributions and community structure. The CLIMAP programme (Cline & Hayes, 1976) illustrated just how dramatic the changes have been in the North Atlantic pelagic communities since the peak of the last glaciations, relative to the North Pacific where the effect seems to have been restricted to longitudinal shifts in the biogeographic zones. In the long term, the pattern of continental drift and the opening and closing of deep channels have been major influences in determining inter-oceanic distributions, and the maintenance of these patterns is related to the vertical ranges of the species. For example the opening of the deep channel between Austral-asia and Antarctica which was followed by a general cooling of the deep waters (Shackleton, 1982), has resulted in the progressively greater segregation of warm-water species whereas the deep cold water fauna has probably become steadily more pan-oceanic.

The vertical gradients in environment parameters can lead to the evolution of physiological, morphological and behavioural adaptations which increase an organism's chance of survival within a restricted depth range yet reduce its fitness beyond that range. Shifts in the vertical profile of a limiting parameter will bring a parallel shift in the species's vertical range; unless this vertical shift results in another factor becoming limiting, in which case a boundary to its horizontal range will occur. An example of such adaptations is provided by the mirror-sides of many mesopelagic fishes. These appear to provide an effective camouflage within the depth range, limited at the shallow end by the depth at which the light field becomes totally symmetrical in a vertical sense, and at the deep end by the depth at which bioluminescent emissions become significantly bright relative to in situ daylight intensity (Denton, 1970). Such morphological adaptations often become progressively expressed during larval development and are associated with ontogenetic migrations (e.g. Badcock & Larcombe, 1980). Such adaptations which have morphological or anatomical expressions are accessible to study through sampling strategies designed to study vertical distribution, but where the adaptation is physiological or behavioural experimental studies are needed to establish the causal factor. In the latter case identification of correlations between biotic and abiotic factors in vertical distribution patterns will provide guidelines for designing the experimental stategy.

As the numbers and geographical coverage of comprehensive vertical studies increase, they are beginning to provide considerable insights into the understanding of horizontal distribution patterns, particularly if the data are properly archived (e.g. Domanski, 1981). Thus two species which are sympatric in a horizontal sense, may prove to be allopatric in a vertical sense. In addition where two similar species overlap in their horizontal ranges, character displacement may lead to their vertical segregation, at least at certain stages of their life cycles (e.g. Angel, 1982). Full vertical coverage of the water column can reveal anomalous geographical patterns which need explanation. An example is seen in the halocyprid ostracod *Halocypria globosa* which off Bermuda dominates the near-surface layers although adult males only occur at deep mesopelagic depths (Deevey, 1968; Angel, 1979). In the N.E. Atlantic it has not been taken pelagically north of 40°N despite quite extensive geographical coverage, but a series of benthopelagic samples taken within 10-100m of the sea-bed on the continental slope at depths of 1000-1600m to the south of the Porcupine Seabight (around 49°N 13°W) contained large numbers of adults (Ellis, pers. comm.). Assuming the Bermudan and Seabight specimens are conspecific, questions arise as to whether the latter are either expatriates possibly carried northwards in the flow of Gulf of Gibraltar water, or if the distributions are distinct or not.

Comprehensive knowledge on vertical distributions at all stages of the life cycle is essential to understanding how the faunas of Mediterranean type seas originate and are maintained (e.g. Alcaraz, 1977; Furnestin, 1979; Vives et al., 1975; Weikert, 1982). For example the occurrence of some of the glacial relict species in the Mediterranean (e.g. *Meganyctiphanes norvegica* and *Benthosema glaciale*) can be understood by extrapolating present distributions to the conditions shown to have occurred 15,000 BP by the CLIMAP programme (Cline & Hayes, 1976). These Mediterranean populations may have become reproductively isolated from the other stocks now found in boreal waters and in the N.W. African upwelling region, through their adaptation to the warm deep water of the Mediterranean. Then if either climatic conditions were to fluctuate again so that the populations would become sympatric, or shifts in the larval ecology should occur which could then allow the passage of stocks into or out of the Mediterranean via the currents systems in the Straits of Gibraltar (Gascard & Richez, 1985), the sibling stocks would become sympatric but fail to interbreed; such a mechanism may help to explain the high species richness of pelagic communities.

Apart from the land masses, the main potential barriers to geographical ranges are oceanic fronts at which there are major changes in the physico-chemical and biological structure of the water column. Too little attention has been paid to the role of fronts in determining distribution patterns at all scales of interaction (e.g. the influence of mesoscale features, see Angel & Fasham, 1983). So long as the conditions do not become lethal across a front, the length of the organism's generation time relative to the persistence and the predictability of a front will determine whether its response is by population growth or behavioural. Wiebe and Boyd's (1978) observations on *Nematoscelis megalops* illustrate how a species's vertical range may gradually shift within a decaying ring, so that it persists only as an expatriate non-breeding population. However, the degree of change in physical characteristics across a front may determine its influence on the community structure. For example preliminary data from a front to the south-west of the Azores (Gould, 1985; Fasham, Platt, Irwin & Jones, 1985) show that although the specific composition of the pelagic community changes very little (Pugh, 1975; Angel, 1979), there were major changes in the pattern of dominance and in the vertical structuring of the community biomass (Angel, 1985). In this example the physico-chemical changes across the front must have been too minor to limit the ranges of the vast majority of species examined. This raises the question as to how well-defined a front has to be to become a major biogeographic boundary.

The clearest signal is probably generated at the subtropical convergences, where permanent stratification and persistently high near-surface stability of the water column occur on the low-latitude side, and there is a seasonal cycle of stratification and water column stability (Robinson, Bauer & Schroeder 1979), and hence primary production, on the high latitude side. Associated with these changes, which produce sharp shifts in the degree of seasonal pulsing of production, are major quantitative and qualitative shifts in the structure and function of the pelagic ecosystems. This influence probably extends, albeit attenuated, right down to the sea bed. Some idea of the speed at which signals of events at the sea surface can be transmitted down through the water column and hence the degree to which the boundary effect may be blurred or displaced by diffusion and advection, is given by the recent results from sediment traps (e.g. Deuser, Ross & Anderson, 1981) and time-lapse cameras deployed on the sea floor (Billett, Lampitt, Rice & Mantoura, 1983). Even so, there are species which are sufficiently adaptable to cross the boundary by adjustment of their vertical range (by submergence) while others are not (Fig. 1). Deeper-living species seem able to cross such boundaries more readily than the shallower-living. However, this may be simply because deeper-living species tend to have more extensive depth ranges, and merely have to restrict their range to be able to cross the frontal zone.

CONCLUSION

Detailed vertical distribution studies are not only useful in trying to understand biogeographic distributions, but are essential to explain many aspects of these patterns and to give pointers to their mode of development.

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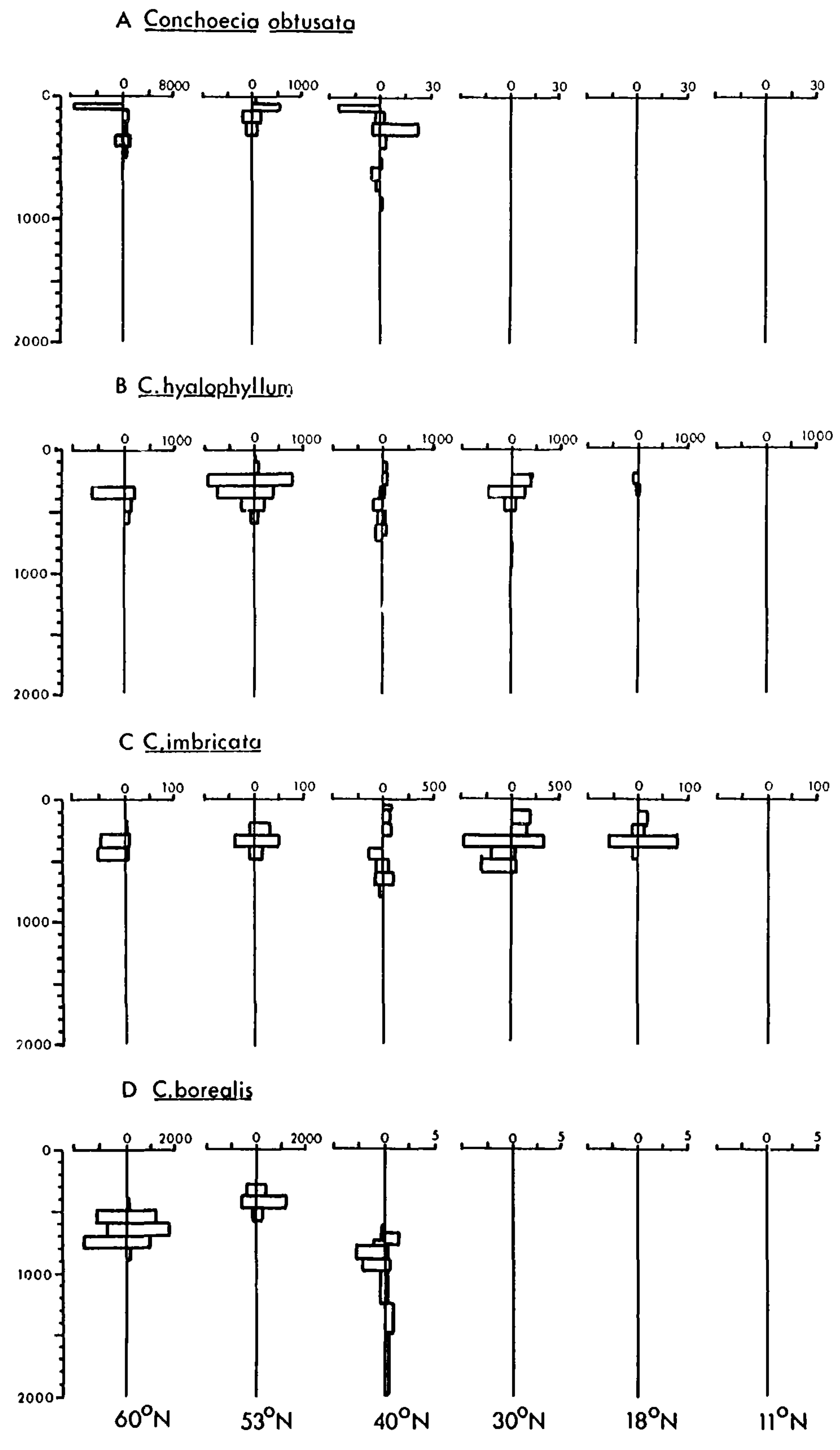
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Fig. 1 Vertical distributions of four species of planktonic ostracods at six stations approximately along 20°W, with day profiles to the left and night profiles to the right. A). *Conchoecia obtusata* a northern species showing only slight evidence of submergence; B). *C. hyalophyllum* a species associated with North Atlantic Central Water which shows changes in its diel vertical migration behaviour with latitude; C). *C. imbricata* another species associated with NACW and showing even greater changes in its intensity of diel migration; D). *C. borealis* a northern species showing clear evidence of submergence. Note the abundance scales vary between profiles.

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BIOGEOGRAPHIC BOUNDARIES IN THE OPEN OCEAN

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INTRODUCTION

It is assumed that the distribution of plants and animals in the pelagial is directly related to the physical properties of the ocean or indirectly to them through so-called biotic factors: the effects of species upon one another. Thus, biogeographic boundaries are taken to be actual physical boundaries such as lie between water masses and their subdivisions; I mean the term "water mass" to be interpreted in a very general way.

The search for the factor (or the few factors) that explains the distribution of a species or narrow group of species of pelagic plants or animals has rarely, if ever, been succesful. Surely it is a complex of factors that exerts the control, the whole suite of properties that a column of water possesses acting in concert, the individual elements being scarcely separable from one another.

BIOGEOGRAPHIC REGIONS

What we really care about knowing is why a certain species is distributed in the way that it is, or conversely, why a certain homogeneous part of the ocean supports the complex of plants and animals that it does. The simple description of the range of this or that plant or animal, a necessary preliminary in which many of us engage, is of limited interest in itself.

One rarely has adequate biological collections for describing the range of a pelagic organism well on the basis of those collections alone. But if the ranges of organisms are controlled by physical factors, then physical description of the ocean (which is more extensive than biological description) can be enlisted in the service of biogeography. The distribution map of an abundant species (Abundant species are the species from which we best learn), is often suggestive of the physical basis of the distribution in water-mass and circulational terms (Fig. 1), and extrapolation of the organism's occurrence from the sampled to the unsampled parts of a physically homogeneous body of water is a reasonable procedure in tentatively describing its range when such a description is needed.

The sudden appearance, disappearance, or radical change in abundance of an abundant organism in collections made along a transect

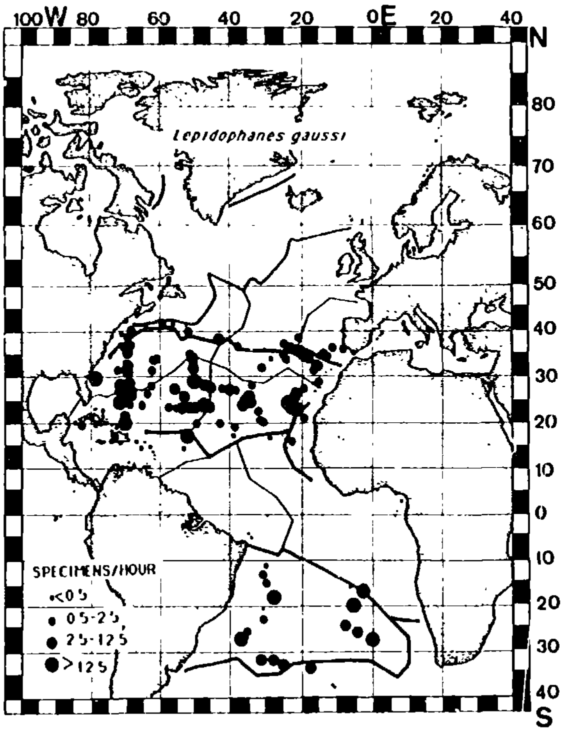


Fig. 1 Distribution of the myctophid fish *Lepidophanes gaussi*, an inhabitant of the subtropical seas of the Atlantic. The diameter of the filled circles is proportional to catch rate. Re-drafted from Backus et al. (1977).

indicates a boundary, biogeographic and physical, and its basis in physical terms often can be assigned. By such procedures physical boundaries that are also biogeographic boundaries have been identified and from these physical boundaries a general framework for pelagic plant and animal distribution can be constructed.

It cannot be expected that a biogeographic boundary in the open ocean will be very sharp. Not only are the physical boundaries upon which the biogeographic ones depend not very sharp, but also a spectrum of responses to a physical boundary by organisms would be expected even were the physical boundary sharp. Nevertheless, it is convenient when speaking of plant and animal distribution to think of a boundary as a line and not to speak of a boundary as an area within which an organism can range. (An indivisible area is delimited by boundaries; it does not contain boundaries; and the range of an organism cannot be said to be boundary-less).

It is my belief that the tentative patterns of distribution for pelagic organisms have been proliferated too much. Often this comes from taking too seriously differences in distribution whose origin actually lies in the imperfection of the data. This is an especial hazard when one uses, not his own data, but the published data of others. The absence of a species in an expected place is sometimes merely the want of the right sort of collecting effort there. The presence of a species in an unexpected place is sometimes merely the result of a few expatriate specimens (waifs) that would have been disregarded had the data set that was used expressed relative abundance. There are many other sources of difficulty including misidentification and taxonomic confusion and some not so simple as these.

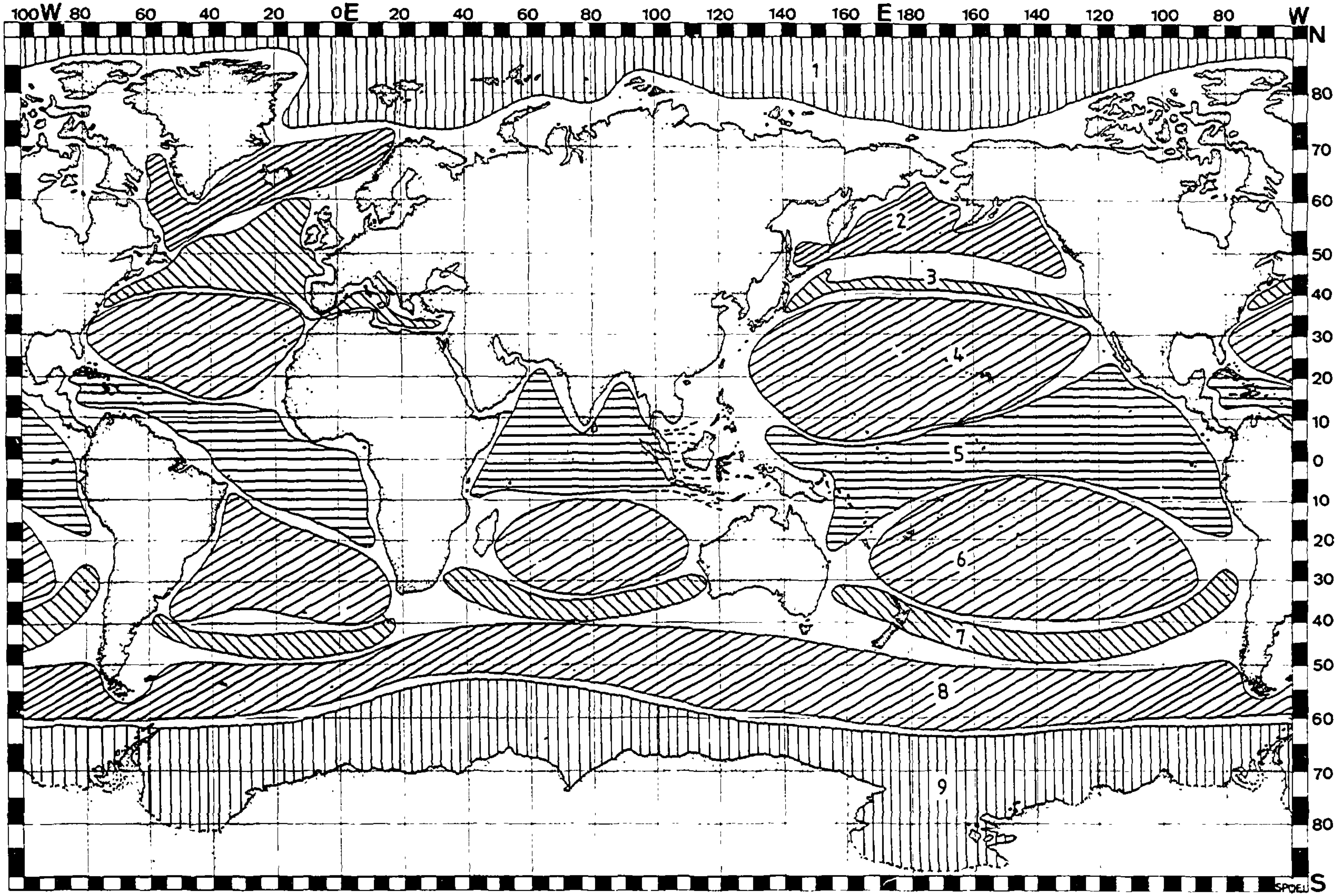
I believe that there may be general enough agreement about the bold outlines of plant and animal distribution in the pelagial so that there can be erected a fairly simple framework to which individual plant and animal distributions can be rigorously compared. By "rigorously" I mean carefully taking into account all the imperfections of the data. Only when the framework cannot accomodate a set of data compared in this way should the framework be elaborated. Such a framework is presented for the world ocean as a map (Fig. 2) and as a diagram (Fig. 3). It is purposely kept very simple for the time being.

In figure 3 solid lines represent the boundaries of biogeographic regions; broken lines divide regions into provinces. Few of the latter have been attempted and, for the moment, definitions are not given for "region" and "province" save to say that the latter is a subdivision of the former. North is at the top of the diagram. Beginning there, the diagram is divided latitudinally into nine regions: Arctic, Subarctic, northern Temperate (or northern Transitional), northern Subtropical (or northern Central), Tropical, southern Subtropical (or southern Central), southern Temperate (or southern Transitional), Subantarctic, and Antarctic. An Arctic region might be omitted, as the Arctic Ocean appears not to have a regular pelagic biota. The term "Transitional" should be abandoned as it is both ambiguous and insufficiently descriptive. I feel particularly uncertain about arrangements at the southern end of the diagram.

The only latitudinal division of the biogeographic regions into provinces is the division of the northern and southern Subtropical regions into poleward and equatorward halves. These provincial boundaries, which in some oceans have been called Subtropical fronts (Roden, 1975), divide the westwind part of each of these regions from the tradewind part of each. The Subtropical front in the North Atlantic often has been called the "northern Subtropical Convergence" ("nordliche subtropische Konvergenz", Wüst, 1928), but it is not the homolog of the subtropical convergence of the southern hemisphere, which is the regional boundary between the southern Subtropical and southern Temperate regions (Veronis, 1973).

The biogeographic regions can be divided

Fig. 2 Map of biogeographic regions of the world ocean. The boundaries drawn are approximate. 1 - arctic, 2 - subarctic, 3 - northern temperate, 4 - northern subtropical, 5 - tropical, 6 - southern subtropical, 7 - southern temperate, 8 - subantarctic, 9 - antarctic.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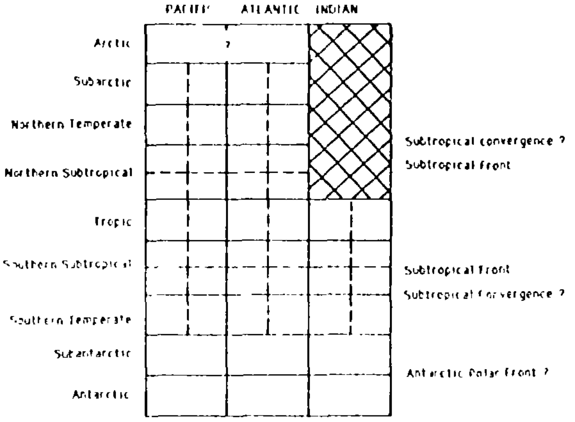

Fig. 3 A partial diagram of the biogeographic regions and provinces of the world ocean. Some detail has been omitted, but in any case knowledge is insufficient for drawing an even approximately complete diagram. Regional designations are at the left, oceans across the top. Certain more or less permanent fronts taken to be boundaries are shown at the left. About the last there is much uncertainty. See text.

meridionally into eastern and western provinces, although no such division is made for the regions of the Southern Ocean, which is viewed as comprising the Subantarctic and Antarctic ones. It might be argued that the southern Temperate region should also be included in the Southern Ocean and that the division of this sea into Pacific, Atlantic, and Indian regions should not be maintained. The east/west division of regions is a gross simplification and simply acknowledges that there are differences in the physics of the east and west sides of oceans (Wooster & Reid, 1962).

The framework of biogeographic regions and provinces given here is purposely kept simple. A possible scale of subdivision is suggested by the scheme of regions and provinces given by the author and colleagues for the Atlantic Ocean (Backus et al., 1977). In addition to the Atlantic regions given in the present work two special regions were established - the Gulf of Mexico and the Mauretanian Upwelling. The most divided region, the North Atlantic Temperate, was apportioned among six provinces - Slope Water, Northern Gyre, Azores/Britain, Mediterranean Outflow, Western Mediterranean, and Eastern Mediterranean ones.

BIOGEOGRAPHIC PATTERNS

It is obvious that the units of geographic distribution (regions and provinces) are not to be equated with ranges or distribution patterns. (When a range is occupied by two or more species of plants or animals, it can be called a pattern.) Rather, the regions and provinces are elements from which, by their varied occupancy by species of plants and animals, diverse ranges and patterns come into existence. Not all combinations are possible - many of the ranges, got simply by variously combining the 23 provinces of figure 3, are inconceivable. No organism would occupy the combined western Pacific Subarctic and western Indian tropical provinces, for instance. Nevertheless, the number of actual or probable combinations seems large.

The point has often been made that the patterns of distribution shown by one group of plants or animals can be quite different from the patterns shown by another group. This is quite so. However, it appears that the system of units of geographic distribution, that is, the regions and provinces, does not change from one group of species to another. Thus, David C. Judkins (unpubl.) saw certain distribution patterns among the decapod crustaceans that were not seen by me and my colleagues among the Myctophidae coming from the same collections (Backus et al., 1977), although the system of biogeographic regions and provinces worked out from the Myctophidae appeared to be equally useful in describing the distribution patterns of the decapods. Similarly, I and my colleagues see distribution patterns among the Gonostomatidae (sensu lato) not seen among the Myctophidae but which conform well to the system of regions and provinces derived from studying the latter.

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BIOGEOGRAPHY OF THE SOUTHWESTERN ATLANTIC; OVERVIEW, CURRENT PROBLEMS AND PROSPECTS

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INTRODUCTION

The Soutwestern Atlantic (SWA) is one of the least studied areas of the world Ocean (see D. Boltovskoy, 1979). Therefore, much basic descriptive work is needed before this area can be subject of more or less ample and comprehensive biogeographic studies. However, a retrospective glance at the advances over the past decades and comparison with the results achieved elsewhere can yield some reflections on the implications of the methods used, the aims of the investigations performed, and the biogeographic significance of the results achieved. The review and discussions that follow are based on an ecological prospective inasmuch the divisions analyzed are assumed to separate discrete communities or ecosystems.

Figure 1A outlines the general hydrological setting of the area. Figure 1C illustrates the water masses present in the area as recognized by distinctive TS curves (Fig. 1B). A review of the biological features of the SWA is given by D. Boltovskoy (1978, 1981).

OVERVIEW OF THE BIOGEOGRAPHIC MODELS PROPOSED FOR THE SOUTHWESTERN ATLANTIC

One of the first biogeographic charts of the oceans which included the SWA, based on zooplankton, was published by Meisenheimer in 1905 (Fig. 2A). Steuer modified Meisenheimer's pattern (Fig. 2B). The chart published by Hentschel 15 years later (1938; 1942) already included all the areas that are usually distinguished today (Fig. 2C).

Subsequent studies, both biological and physico-chemical, contributed to describe the boundaries and assess their seasonal displacements, and further characterize the main zones by their abiotic parameters and typical biological assemblages. But the draft proposed over 40 years ago did not undergo radical changes. On the other hand, figures 3 and 4 show that, as far as the locations of the boundaries are concerned, the agreement is rather poor, and this lack of coincidence does not seem to decrease with successive studies (Fig. 3).

These biogeographic patterns are similar inasmuch they all distinguish warm-water from cold-water assemblages, and several further divide each of these into two sectors. The limits between areas, however, vary widely (Figs. 3 & 4). Furthermore, the Transition is absent from over half of these schemes.

SPECIES' DISTRIBUTION PATTERNS, WATER MASSES AND BIOGEOGRAPHY

In oceanography, biological indicators have been used in two different ways: as tracers of water movements, and as sensors of oceanographic parameters. The difference between these two applications is subtle: sometimes they are closely interwoven or even overlapping. E. Boltovskoy (1967) concluded that, among other requirements, an adequate tracer should be fairly - but not extremely - sensitive to ecological parameters: it should be sensitive enough not to inhabit more than one of the currents or water masses that are under study in a particular area, but not as sensitive as to disappear from its habitat as soon as environmental conditions change slightly.

The "biological tracer method" has been used regularly for biogeographic purposes, thus assuming tacitly that the end of a given current (that is, of its tracers) is coincident with a biogeographic boundary. However, this may or may not happen, and the underlying assumptions can be valid in some areas, but not in others. The

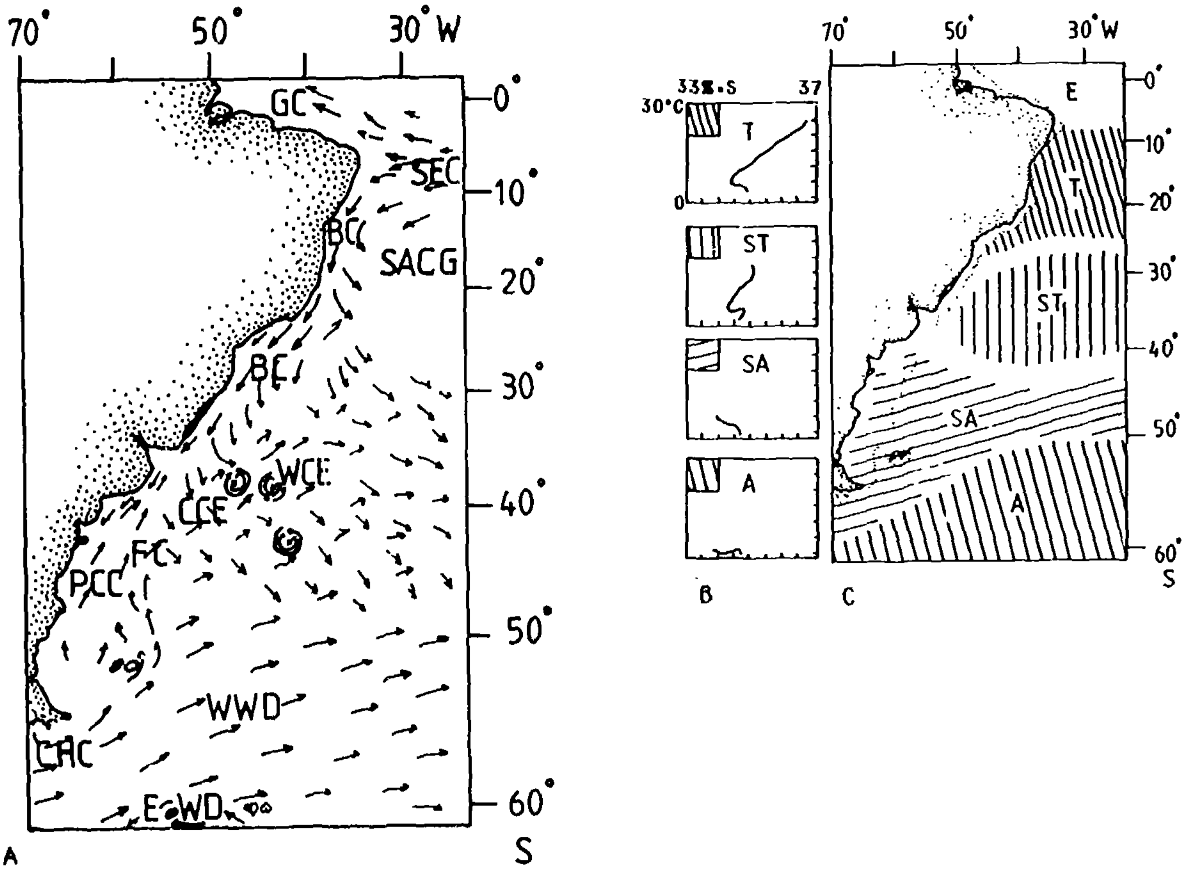


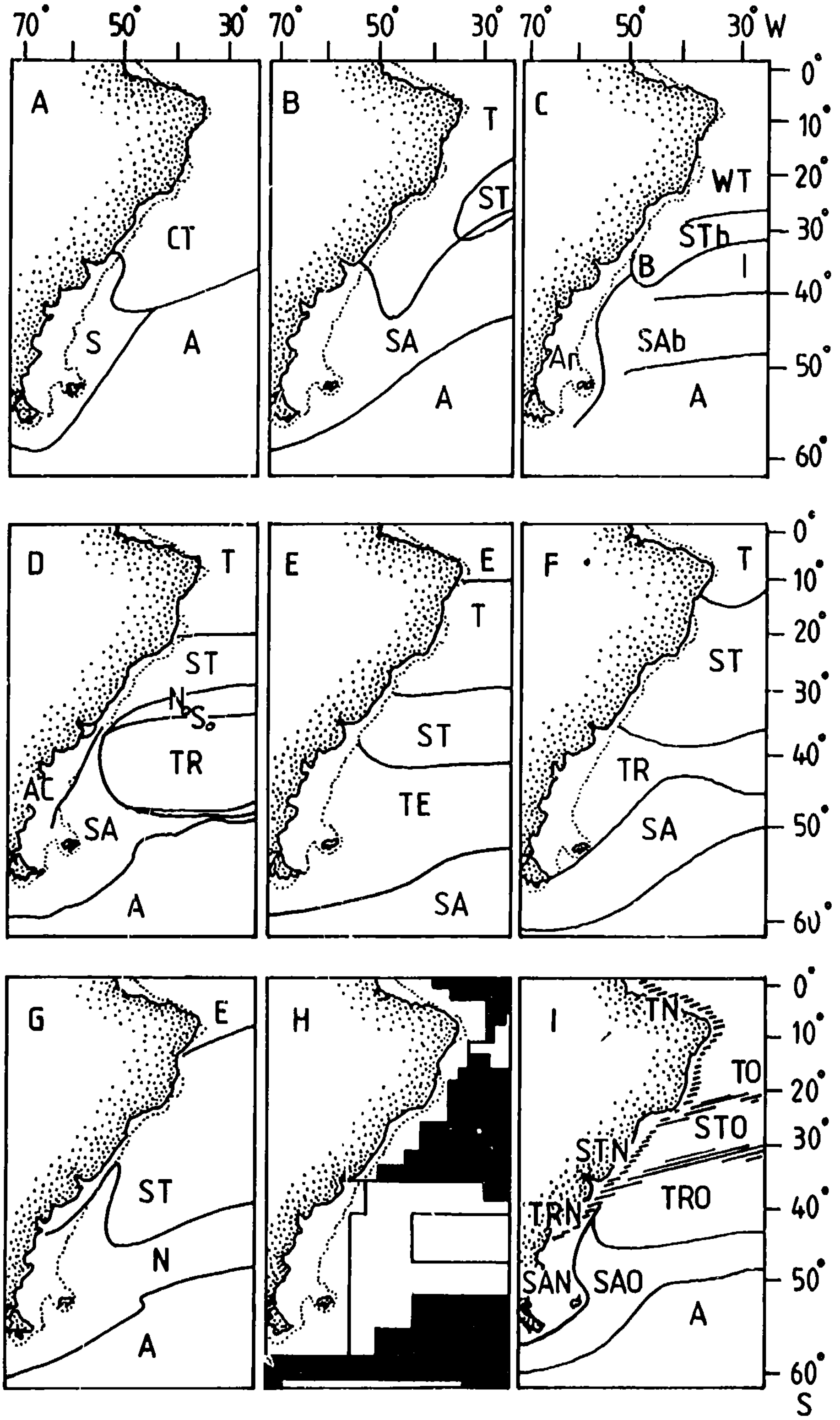
Fig. 1 Currents (A) and water masses (C) with their corresponding typical TS curves (B) in the Southwestern Atlantic. BC : Brazil Current; CCE : cold-core eddies; CHC : Cape Horn Current; EWD : East Wind Drift; GC : Guiana Current; FC : Malvinas (=Falkland) Current; PCC : Patagonian Coastal Current; SACG : South Atlantic Central Gyre; SEC : South Equatorial Current; WCE : warm-core eddies; WWD : West Wind Drift. (A: compiled from different sources; B & C : from Gorshkov, ed., 1977).

criterion of the goodness of a tracer is usually derived from hydrological patterns established on the basis of physical studies. In other words, an organism is considered a good tracer if its distributional range matches adequately the known or suspected course of a current, and it still survives in its waters when these are no longer distinguishable by their physical parameters. Thus, its distribution indicates the influence of a current, the extension of a physical phenomenon, but not necessarily a major biological break (Fig. 5).

On the other hand, the species that are snugly restricted to a single water mass are considered biological indicators (=sensors) of the latter. As opposed to tracers, the environmental tolerance of sensors has to be relatively narrow; their distribution should match a more or less homogeneous TS envelope, rather than a current which can undergo wide temperature and salinity changes along its route.

In addition to water mass-related conclusions, work with tracers and sensors interleaves intimately with biogeography. Thus, indicator species initially selected for their fidelity to a current or to certain temperature and salinity ranges end up being the main material for defining biogeographic areas. This happens so frequently and to such an extent that it often is difficult to discern whether a particular report is dealing with water masses or with biogeographic areas.

In many of the investigations which include all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or most of the species belonging to one or more higher level taxa (as opposed to those that deal with indicators only), a major point is made of analyzing closely the relationship between water masses and planktonic distributions. Thus, individual species' ranges are examined "from a water mass point of view" and the conclusion is commonly reached that water masses account for the general patterns adequately.

A tacit, and sometimes explicit, implication of these results is that since most species show clear affinities for given water masses, ergo their distribution boundaries match water mass limits. There are many examples to support this assumption. However, a closer look at this relationship shows that, although there is an evident tendency for the species' boundary lines to be denser at the water mass limits, most of them fall actually within water masses, rather than on boundaries between them (e.g., planktonic Foraminifera in the SWA, cf. E. Boltovskoy, 1981b, Fig. 163; Euphausiaceae in the Pacific, cf. Brinton, 1962, Fig. 101). Figure 6 suggests that these mismatches are especially obvious when detailed charts (rather than schematic simplifications) are available.

Figure 7 shows that, when total ranges are compared, the great majority of the species are not found in all sectors of the water mass that they inhabit, very few extend throughout an entire water mass, and even fewer are effectively restricted to a water mass. There are some endemics (especially in the Subarctic area), but practically none is an endemic **and** is found throughout the entire water mass.

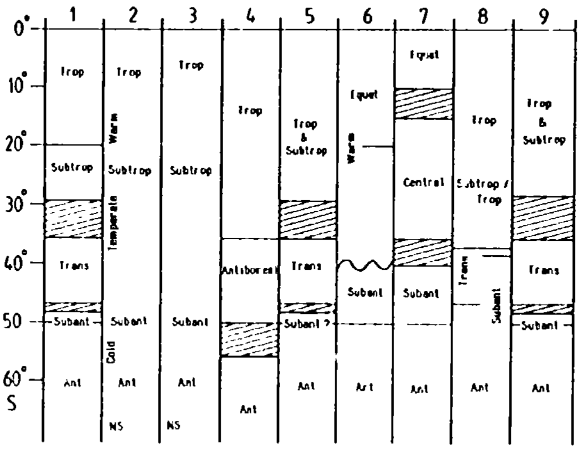


Fig. 3 Approximate limits of distinctive faunal planktonic assemblages in the Southwestern Atlantic (pelagic waters). 1 : Foraminifera (E. Boltovskoy, 1970a;1981a,b); 2 : Tintinnina (Souto,1981); 3 : Siphonophorae (Alvariño, 1981); 4 : Hydromedusae (Ramirez & Zamponi, 1981; based on Kramp, 1957); 5 : Pteropoda (Van der Spoel & Boltovskoy, 1981); 6 : Ostracoda (Angel, 1981); 7 : Copepoda (Bjornberg, 1981); Euphausiacea (Antezana & Brinton, 1981). NS : limits between zones not specified.

Reviews of the information available suggest not only that most species cross water mass boundaries regularly, but that plankters evidence a clear tendency to inhabit more than one water mass. Table I shows an example of the distribution of the species of some taxa between the cosmopolitan, moderately broad and endemic types (see also Venrick, 1971; Reid et al., 1978; Van Soest, 1979).

In the light of these considerations, table II and figure 8 summarize the distribution types of

Fig. 2 Major biogeographic zonations of the southwestern Atlantic Ocean according to different authors.
Zones: A= Antarctic; AC= Argentine coastal; Ar= Argentine; B= Brazilian; CT= circumtropical; E= Equatorial; I= intermediate; N= notalian; No= northern limit; S= Southamerican; SA= Subantarctic; SAb= Subantarctic boundary; SAN= Subantarctic neritic; SAO= Subantarctic oceanic; So= southern limit; ST= Subtropical; STN= Subtropical neritic; STb= Subtropical boundary; STO= Subtropical oceanic; T= Tropical; TE= Temperate; TN= Tropical neritic; TO= Tropical oceanic; TR= Transitional; TRN= Transirional neritic; TRO= Transitional oceanic; WT= western Tropical.
Sources: A= Meisenheimer (1905); B= Steuer (1933); C= Henschel (1938); D= Boltovskoy (1959); E= Bogdanov (1961); F= McIntyre & Bé (1967); G= Nesis (1974); H= Pierrot=Bults & Van der Spoel (1979); I= Dadon & Boltovskoy (1982).

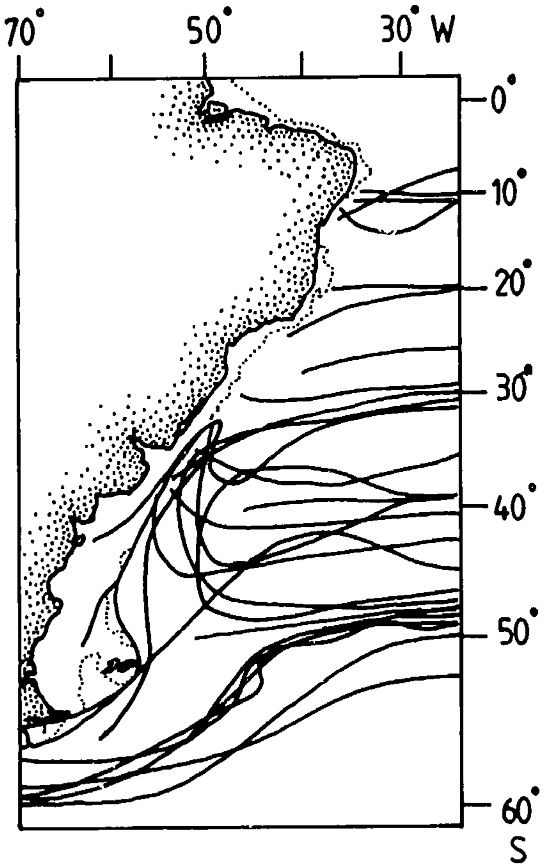
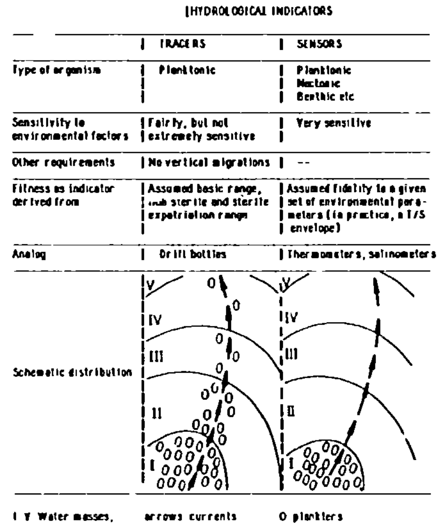


Fig. 4 Composite sketch of the biogeographic boundaries illustrated in Fig. 2C-I.

oceanic plankters in terms of water masses and their boundaries. The fidelity concept is that of Boltovskoy, 1967 (as referred to water mass indicators), and of Fager, 1963 (as referred to communities), with the additional restriction that the species must effectively occupy **all** the area concerned. Fager' s (1963) "vitality" and "periodicity" criteria are, in this context, two aspects of the abundance concept.

The results reported (see reviews in Johnson & Brinton, 1963; Beklemishev, 1959; McGowan, 1971), achieved after the analysis of thousands of samples leave little doubt that there effectively is a strong affinity of most of the species treated for specific areas of the ocean. However, their individual sensitivity to the boundaries established by means of physical studies is fair at best.


HYDROLOGICAL INDICATORS

	TRACERS	SENSORS
Type of organism	Planktonic	Planktonic Nectonic Benthic etc
Sensitivity to environmental factors	Fairly, but not extremely sensitive	Very sensitive
Other requirements	No vertical migrations	--
Fitness as indicator derived from	Assumed basic range, sub sterile and sterile expatriation range	Assumed fidelity to a given set of environmental parameters (in practice, a T/S envelope)
Analog	Drift bottles	Thermometers, salinometers
Schematic distribution		

I V Water masses, arrows currents O plankters

Fig. 5 Summary of the basic differences between hydrological tracers and sensors.

BIOGEOGRAPHIC ZONATIONS, TRANSITION ZONES AND COMMUNITIES

Starting in the 1950' s, analyses of the vast information accumulated on the distribution of oceanic plankton showed that recurrent biological assemblages are linked to specific segments of the ranges of variation of some parameters other than temperature and salinity. Among these are phytoplanktonic primary production, zooplanktonic standing stock, vertical stratification and migration patterns, endemism, equitability, particle size, food web characteristcs, seasonal production variations, metabolism, turnover rate (Vinogradov, 1968; Koblentz-Mishke et al., 1970; Bogorov, 1974; McGowan, 1971; 1974; Conover, 1979; etc.). These distinctive functional features gave grounds for concluding that the assemblages in question are fairly independent ecological units: communities or ecosystems.

Co-occurrence is a necessary, but not sufficient, requirement for the community concept. The co-occurring organisms must be also functionally interrelated. A cutoff value can be given by the condition that relationships within a community are closer than those with members of

Table I Approximate numbers of species of some zooplanktonic groups present in the surface waters of the southwestern Atlantic (modified from Boltovskoy, 1978).

	Antarctic		Subantarctic		Subtropical* & Tropical		Cosmopolitan (at least Subant. and Subtropical)	Total spp.
	P	R	P	R	P	R		
Foraminifera	5	0	12	2	30	10	2	35
Pteropoda**	3	-	9	2	50	46	4	62
Chaetognatha	6	0	11	2	20	12	7***	26
Salpidae	3	2	5	2	17	15	2	20
Appendicularia	23	7	14	0	30	14	14	35
Totals	40	9	51	8	147	97	29	178
% of total in SWA	22	5	29	4	83	-	16	-

*Almost all these species inhabit both areas

** Subspecies, formae and morphae computed separately

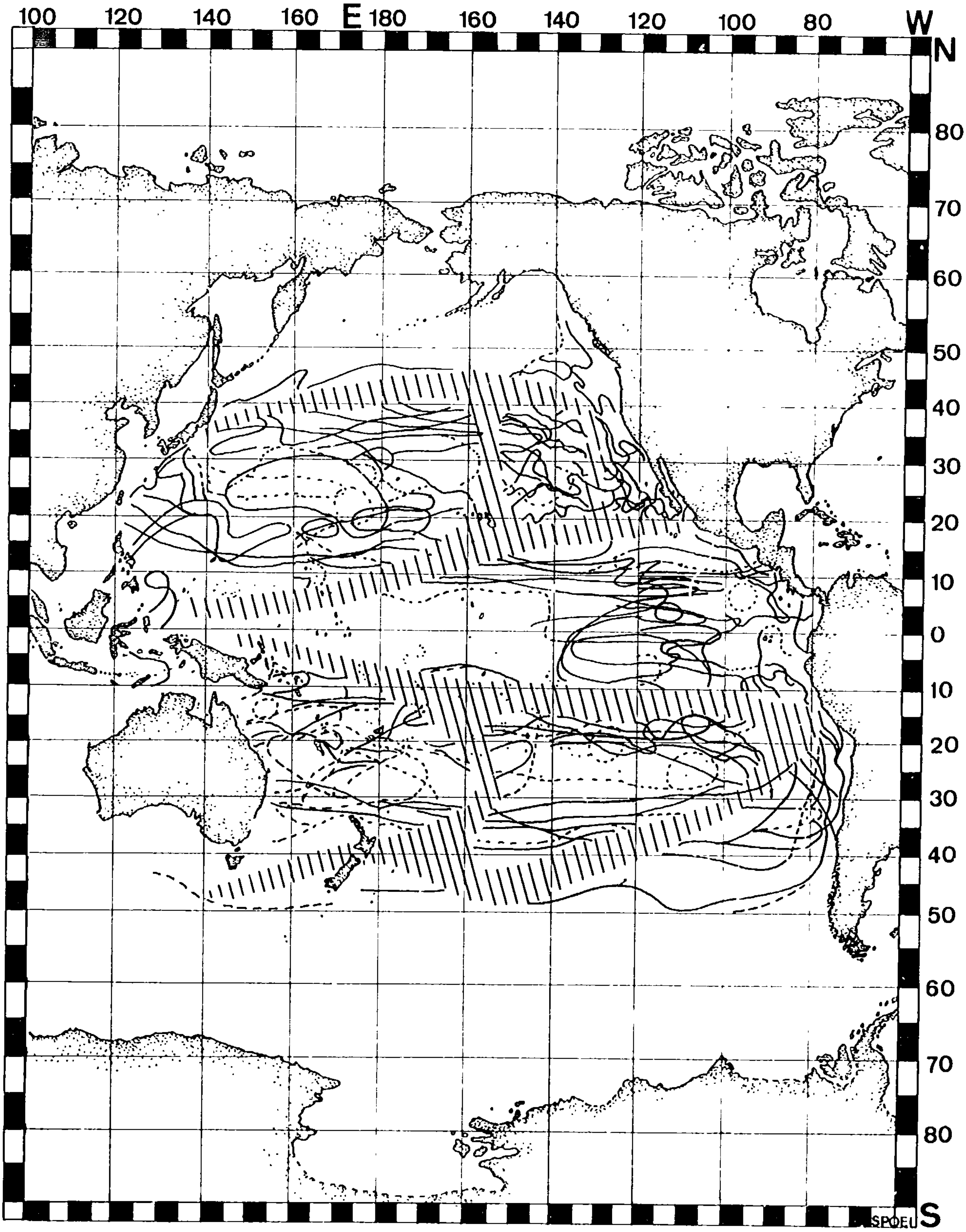
*** All meso and bathypelagic at mid and low latitudes

P= present; R= restricted (endemic)

Table II Some attributes of the distribution types of planktonic organisms illustrated in figure 8.

Distribution type in figure 8	Fidelity to		Fitness as indicator of			Frequency in plankton
	B	C	B	C	B/C limit	
1	+	-	+	-	+	-
2	-	+	-	-(+)	-(+)	-
3	-	-	-	-(+)	-	-
4	-	-	-	-	+	-
5	-	-	-	-	-(+)	-
6	-	-	-	-	-	-
7	-	-	-	-	-(+)	++
8	-	-	-	-	-	++
9	-	-	-		-(+)	+(?)
10	-	-	-	-	-(+)	+
11	-	-	-	-	-	-

-(+): Not adequate, but can be used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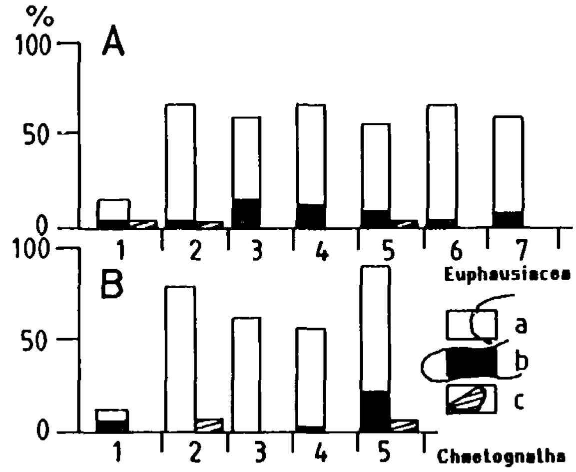

Fig. 7 Percentages of taxa (totals, Euphausiacea: 38, Chaetognatha: 18) present in part of the water mass (white, A), in the entire water mass (black, B), and restricted to the water mass (not occurring in other water masses, but not present in all parts of this one (hatched, C). 1 : Subarctic; 2 : Western North Central; 3 : Eastern North Central; 4 : Transition; 5 : Equatorial; 6 : Western South; 7 : Eastern South. (Based on distribution charts by Brinton, 1962; Bieri, 1959).

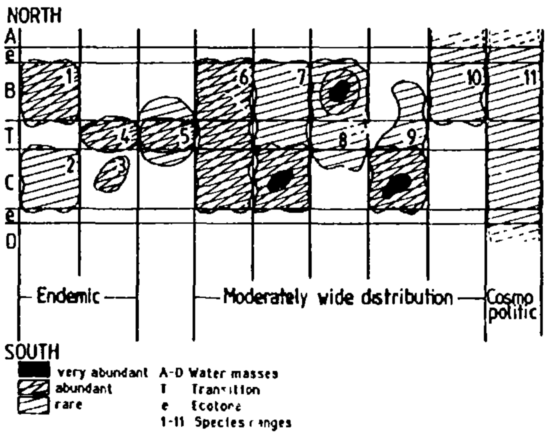

Fig. 8 Schematic diagram of the distribution ranges of planktonic organisms as referred to water masses (see also Table I).

other communities. In most major oceanic systems semi-closed recirculating patterns allow the organisms to maintain their ranges, reproduce and, probably, evolve jointly (see, however, Margalef, 1967; Haedrich & Judkins, 1979; Van der Spoel & Heyman, 1983). In contrast, Transition zones seem to be quite different in this respect.

In the Transition zone of the SWA most Subtropical and Subantarctic species consistently occur in the area. Some show incipient adaptations to these local conditions (see Van der Spoel & Boltovskoy, 1981); but have their distribution centers elsewhere; and a few species with broader total ranges have maximum densities in the Transition, for example, the foraminifera *Globorotalia truncatulinoides* and *G. inflata* (E. Boltovskoy, 1981b).

But Subantarctic and Subtropical expatriates make up anywhere from 70-80 to >90% of the overall inventory. Given the fact that they are expatriates from other systems it is safe to assume that they are not adapted to the Transition. Samples collected in this area usually have very high proportions of juveniles (Pteropoda), sexually immature (Chaetognatha), and deformed (Foraminifera) specimens; this strongly suggests that the expatriates do not reproduce here (Margalef, 1967). Therefore, there most probably is not genetic specialization and one can assume that their interrelationships are neither as frequent nor as specialized as the ones they maintain with members of their original communities, within the latter. Even the ties between organisms of identical procedence can be expected to be looser here than in their original media: environmental differences and mixture with an heterotopic assemblage can modify the physiological and ethological responses considerably (e.g., lack of mating).

Fig. 6 Distribution ranges of 26 euphausiid taxa (thin lines) and water mass boundaries (hatched areas) in the Pacific. The species limits coincident with water mass boundaries are not shown. (Redrawn from Brinton, 1962).

On the other hand tho relationship among endemics and of the latter toward the immigrants are probably more firmly established. Figure 9, based on these speculations, suggests that, for overall relationships in the Transition to be comparably close and specialized as in typical communities, endemics and " semi-endemics" should be numerically totally dominant over pooled expatriates; in the SWA this certainly is not the case.

These considerations incline me to conclude that the Transition assemblage is not comparable with full scale communities, although it has a precisely definable biotope, and also some peculiar species. Some of the changes that take place in this type of areas resemble replacements of entire communities, rather than variations within a single community (e.g., Venrick, 1971). Beklemishev (1969) pointed out that Transition areas are in a state of dynamic equilibrium being continuously generated at one end and destroyed at the other.

CONCLUDING REMARKS

Throughout this review I tried to point out and/or furnish evidence of the following:

1. That biological tracers and sensors are adequate tools for some hydrological aplications, but their use can be misleading when working on the biogeography of ecological units. Biologists tend to use indicator species for hydrologic (current and water mass) studies and for biogeographic purposes interchangeable, to the point that in somes cases it is not clear whether a particular zonation proposed refers to water types or to biogeographic areas. These two concepts are not synonymous.
2. That the distribution of most planktonic species and pelagic communities is associated with, but hardly ever restricted to or spread throughout an entire water mass. The match "species distribution - water mass" is poor for the great majority of the plankters.
3. That TS-defined water masses and currents are related with the position and boundaries of pelagic communities, but water mass patterns are not coincident with the patterns of the communities.
4. That transitional assemblages have important functional differences with non-transitional assemblages.

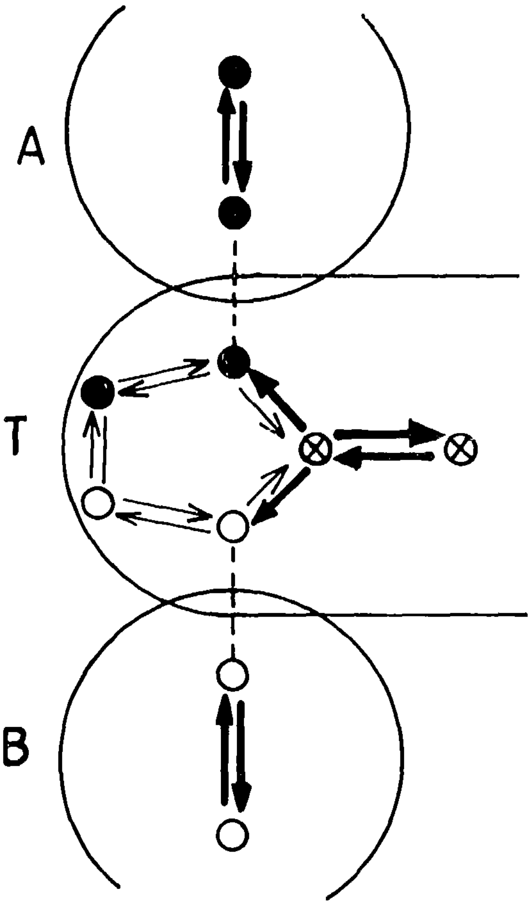

Fig. 9 Hypothetic scheme of the relationships between organisms in planktonic communities (A, B) and in a Transition zone (T). Specialized interactions (thick arrows) are dominant in the former; when members of the communities become expatriates in a Transition, their mutual ties, and especially those with the expatriates of different origin and with local inhabitants become looser and circumstantial (thin arrows). Assuming that the Transition hosts equal proportions of endemics and expatriates of different communities, 2/3 of the interactions are here non-specialized.

For the SWA, with the exception of "Meteor's " work, extensive and thorough distributional investigations were carried out only with Foraminifera. However, these were aimed at the study of circulation patterns, rather than at ecologically oriented biogeographic analyses. Most other schemes seem to have been defined on the basis of " unnatural bounderies" inasmuch the latter exist though an a priori definition (i.e., current and water mass patterns). In consequence, with a few exceptions the coincidences between the latter seem to arise from the acknowledgement of the divisions derived from physical studies, rather than from proven dissimilarities between the distributions and/or abundances of the groups concerned. In fact, for most taxa the information is simply not yet available for any more or less meaningful and thorough analyses.

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ON THE EFFECTS OF INTERANNUAL VARIATIONS IN CIRCULATION AND TEMPERATURE UPON THE EUPHAUSIIDS OF THE CALIFORNIA CURRENT.

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INTRODUCTION

Physical characteristics of ocean water-notably temperature and currents- differ from place to place within a zooplankton species' distributional range (Reid et al., 1978). However, significant departures from temporal regularity in these characteristics within the total system upon which the species depends for reproduction and growth, would, in the course of time, be expected to initiate departures from existing range and from the adaptations normally employed in maintaining range. We have studied the euphausiid crustaceans and their physical environment in the California Current since 1950 and propose, here, to provide examples of changes which have taken place. A recent environmental variation, El Niño of 1983 to 1985, has been as extreme as any observed so far.

The California Current is recognized as being particularly complex biogeographically, encompassing its own warm-temperate and subtropical biotas together with intrusions from the eastward flowing North Pacific Drift, the anticyclonic Pacific Central Gyre, and, to a lesser extent, the zonally maintained equatorial water mass. For this reason, and also because of its variable, meandering nature and, typically, a seasonal reversal of nearshore flow, this current is known as a "system" - the California Current system (Reid et al., 1958). System implies order, however complex.

THE TIME SERIES

For most of this century there are records of temperature, salinity, density, and sea level from the Scripps pier near San Diego, 33°N. These are expressed here as anomalies which are the monthly means minus the long-term monthly mean (Fig. 1). These temperatures are generally well correlated with temperatures in at least that

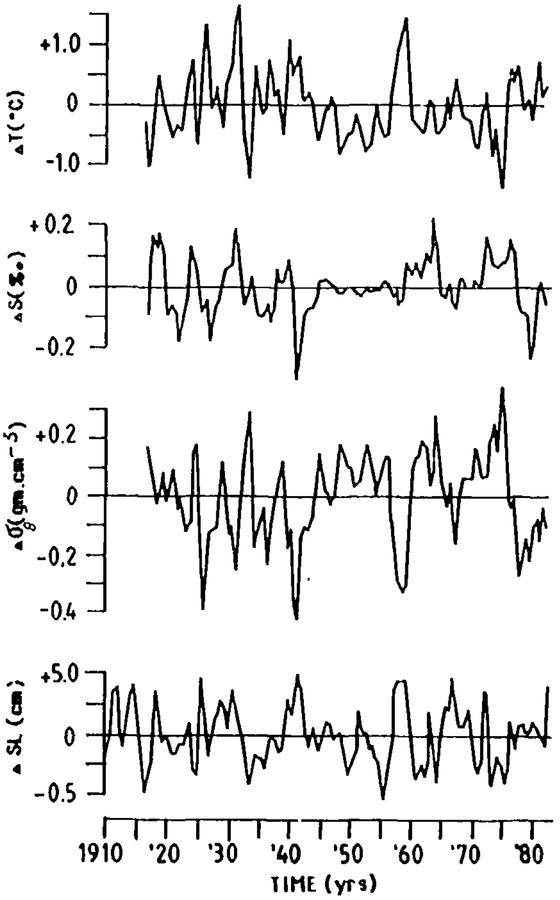


Fig. 1 Six-months running mean time series of temperature, salinity, density and sea-level anomaly at the Scripps pier. Prior to 1925, the sea level data are from the San Diego tide gauge. Sea level was corrected for secular rise and inverse barometer. From Simpson (1985).

part of the California Current which extends along the southern California coast.

The temperature record shows that between 1915 and 1945 there were more warm episodes and of longer duration than cool ones. The recent period, 1945 to present, has been generally cooler than the mean, but with three prominent periods of higher than average temperatures, 1) late 1957 through 1959, 2) 1976 into early 1978 (Brinton, 1981) and 3) 1981 to 1984, possibly into 1985.

THE SPECIES

Four euphausiid species are considered of particular importance in the California Current:

1. *Euphausia pacifica* extends southward from the subarctic zone, almost to the tropics along Baja California during cool periods (Brinton, 1962).
2. The more southern species *Nyctiphanes simplex* tends to exhibit a range complementary to that of *E.pacifica* in the California-Baja California coastal environments.
3. *Euphausia eximia*, in this system , is adapted to "cool productive waters marginal to the equatorial water mass" (Brinton, 1979). These three species migrate vertically between the surface layer and 200 or 300m depth (Brinton, 1967).
4. *Nematoscelis difficilis* occupies the narrow zone of the oceanic North Pacific Drift 40 to 45°N, but, also, nearly the full extent of the California Current, 23° to 43°N; hence it is of limited interest biogeographically within this current.

The particularly extensive range in the California Current occupied by *N.difficilis* and also by another cool-water species, *Thysanoessa gregaria* may be due to their inhabiting depths in and beneath the thermocline (Brinton, 1967). On the other hand, *E.pacifica* enters the mixed layer at night and, therefore, also may be limited toward the south by mixed layer temperatures - as may be the warm-water vertical migrators at their northern limits.

BIOMASS OF EUPHAUSIIDS IN SYSTEM

During the 1983-1984 period of high water temperatures in the California Current, it appeared that euphausiids constituted a higher than usual proportion of the total catches. Therefore, a comparison was made between certain cool and warm periods, using existing euphausiid biomass data (Isaacs et al., 1969; 1971). January 1955 to April 1957 encompassed the cool period of mid-1955 through 1956 (Figs. 1,2a), and mid-1957 through 1959 covered the period which, until 1982-84, was known to us as the "warm years" (Figs. 1,2b).

In winter (January), summer (July), and autumn (October), there was little difference between cool and warm years in euphausiid biomass (all species combined) (Table I). January in both cool and warm periods had the lowest concentration. In April, associated with spring growth to reproductive condition, there was an increase in euphausiid biomass in both cool and warm periods; for the cool period, individual April values were up by factors of 5 to 15 over January, and individual values for the warm period by 3 to 4. Also, the proportion of euphausiid biomass to the total zooplankton indeed was greater in warm periods than in cool periods, by averages of 14, 21 and 21% for January, July and October, respectively, and by 6% in April.

Are the individual species all responding in concert with increases and decreases in biomass, or are there year-to-year differences in proportions of species having different biogeographical affinities- as one would expect? To this end, some events of the recent 1983 to 1984 warm period will be compared to cool 1952 and 1956 (Fig.2a). The 1983 Scripps pier temperatures were above the mean, except in June, while in 1984 they were above the mean except in December (Fig. 2c). Along a line of stations extending westward through the southern California bight past Point Conception (Fig.3a), cool-water *Euphausia pacifica* appeared strongly dominant in April 1956, and was important, even in January (Fig.3b). At the same time, the more southern coastal species *Nyctiphanes simplex* was scarce and the southern, more oceanic species *Euphausia*

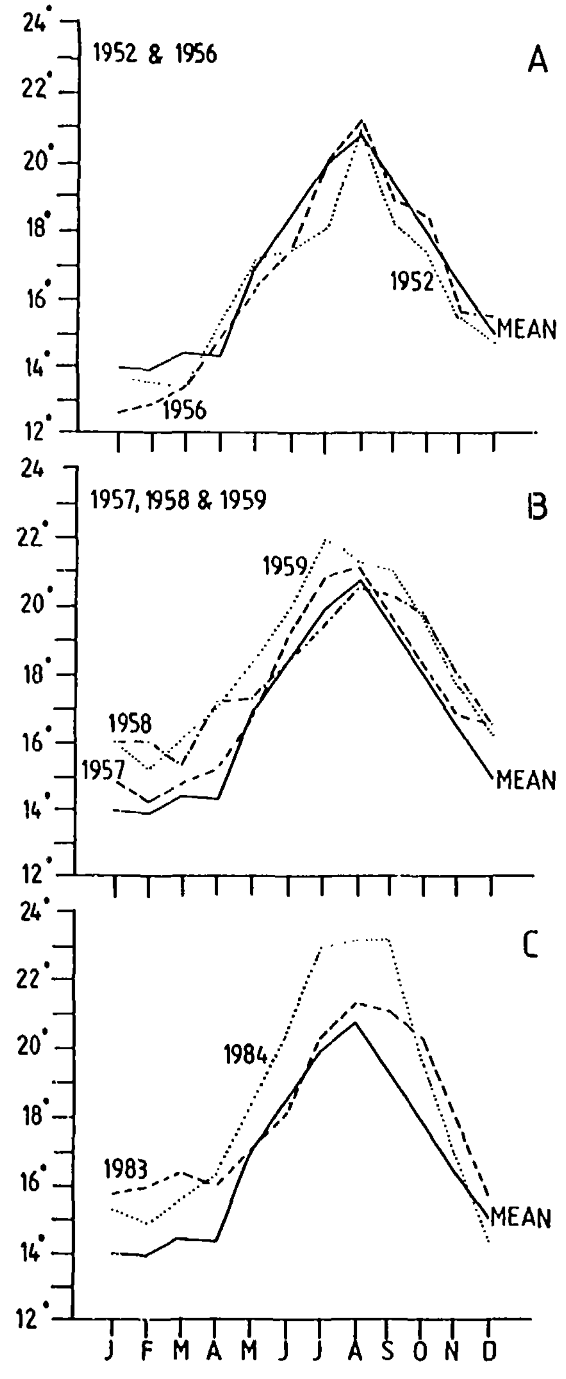


Fig. 2 Scripps pier temperature. Long-term monthly mean (1917-1980) and means for A. 1952 and 1956; B. 1957, 1958 and 1959; C. 1983, 1984.

eximia was absent - evidently not reaching this far north from its usual density center off mid-Baja California, 25-30°N.

In contrast, during 1984 (January, April) *Nyctiphanes simplex* was the dominant euphausiid, particularly inshore (Fig. 3c), while *E. eximia* penetrated the area from the south, as during 1983.

BIOMASS AND DISTRIBUTION

When examining a shift in the limits of distribution of a species, it is useful to consider whether there has been a change in the population density (e.g., as with the Pacific sardine, CalCOFI Rep., 1960: 8-1). High abundance might lead to spreading beyond limits exhibited during times of low abundance. January distributions from 1969, an undistinguished year with respect to temperature, will be compared with the warm Januaries of 1978 and 1984 (Fig. 4).

E. pacifica, in January 1969, extended southward to 30°N, near Guadalupe Island, evidently occupying the main stream of the California Current. In the brief warm period of early 1978 the southern, offshore limit of range had retracted from the 1969 limit only by about 200km, while overall biomass remained nearly the same as in 1969, 1.9g/m^2. In the longer 1983-84 warm period, the January range limit differed little from that of similarly warm 1978, but 1984 mean biomass was much less, 0.2g/m^2, after more than a full year of above-average temperature.

In contrast, biomass of *N. simplex* was about five times higher during the two warm Januaries (1978, 1984) than during January 1969. It should be noted that, during midwinter, northerly flow along the coast is a typical feature of the California Current (Reid et al., 1958). Such flow extends the northern limit of *N. simplex* beyond our sampling grid (Fig. 4), while variation in the offshore limit is better documented.

Evidence that the interannual differences in biomass are largely a consequence of changes in abundance rather than in age structure of the population is to be seen in figure 5. For all body lengths of both species there was, roughly, a tenfold difference in abundance between 1969 and 1984, although in 1984 *N. simplex* seems to

Table I Euphausiid biomass (wetweight)*, as a proportion of total zooplankton biomass, California Current cool period (Jan.1955-April 1957) compared with warm period (July 1957 through 1959)

PERIOD		WEIGHT OF EUPHAUSIIDS gm/m^2		WEIGHT OF EUPHAUSIIDS AS % OF WEIGHT OF TOTAL ZOOPLANKTON		
		X	$\bar{X}$	RANGE	$\bar{X}$	$\bar{X}$ % INCREASE, WARM PERIODS
JANUARY	COOL	2.1, 3.2, 1.1	2.1	17-27	20	14
	WARM	1.1, 1.8	1.5	24-44	34	
APRIL	COOL	9.9, 21.0, 16.7	15.9	42-51	48	6
	WARM	4.6, 5.5	5.0	50-57	54	
JULY	COOL	3.2, 2.9	3.1	7-12	9	21
	WARM	1.9, 3.1, 4.2	3.1	13-46	30	
OCTOBER	COOL	3.1, 4.6	3.8	13-18	15	21
	WARM	2.5, 1.3, 3.1	2.3	29-40	36	

*Values have been adjusted for: 1) observed night/day proportions (CalCofi Atlases Nos. 10, 14, 21), and 2) 1m ring net/ Bongo net catch ratio for Euphausiid biomass, $\bar{X}$= 1/2 (Brinton & Townsend, 1981).

have age groups at 6 and 10-11mm body length which were indistinct in 1969.

Euphausia eximia is not often an important member of the zooplankton off California, usually being south off 30°N in Mexican waters. However, we considered (Fig.3) that its presence off southern California during 1983-1984 was significant evidence that there was northward transport of oceanic as well as of neritic water. *E.eximia* tended to be concentrated seaward of coastal *N.simplex* off Baja California, and extended northward, though not nearly as far as *N.simplex*, during the warm periods of early 1978 and 1984 (Fig. 6). There were corresponding increases in biomass (over January 1969) in the zone north of station line 110 (29°N).

Examples of flow in the California Current during El Niño of 1983 to 1984 show that in early 1983 (Fig.7a), northerly flow from the southern California bight was directed westward, then northward beyond Point Conception. Such flow is clearly associated with the westward bulge of the distributions of species in that region (Figs. 4, 6) observed during early 1984. The southern species, *N.simplex* and *E.eximia*, having shifted northward as the waters warmed, then spread broadly toward the west at the break in the coastline at Point Conception.

The 1983 warming off southern California continued into 1984 (Fig.2c). This was associated with a large, sluggish, oblong eddy situated in and off the bight (Fig.7b). In April 1984, strong, southward flow resumed along central California (35-38°N), but not off southern California (Fig.7c). Anomalies of steric height for cruises during the warm periods 1983 and 1958 better illustrate deviations from means. In early 1983 (Fig.8a) measurements of steric height were above the seasonal mean from central Californian waters to northern Baja California. Highest anomalies were generally nearest to shore, reaching 14 dynamic centimeters to the north of Point Conception and off southern California. Such northward coastal flow resembled that of 1958 (Fig. 8b).

In the above discussion, the relatively numerous euphausiid species (e.g. *Thysanopoda astylata, Euphausia hemigibba, Nematoscelis tenella, Stylocheiron carinatum*)

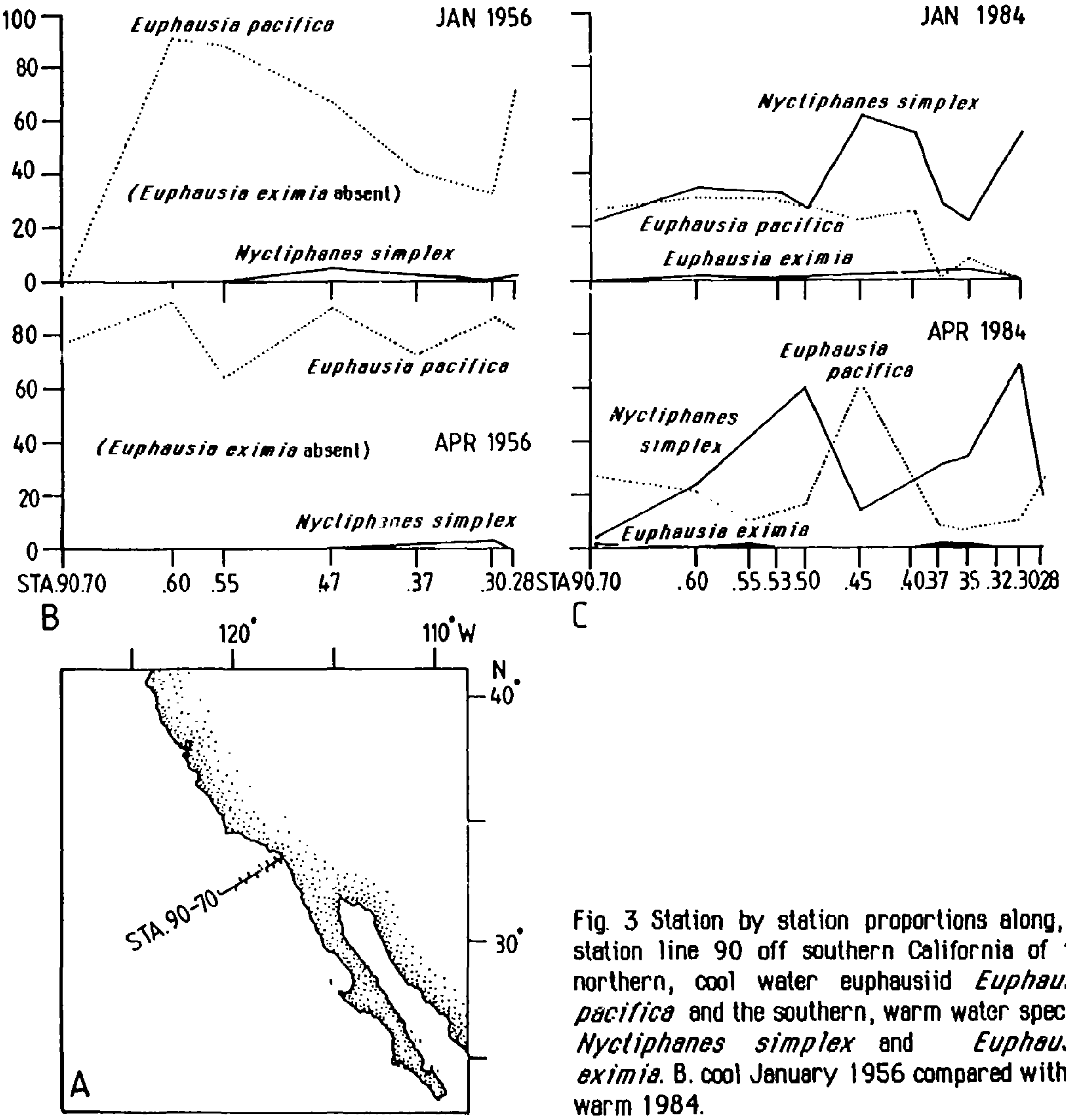
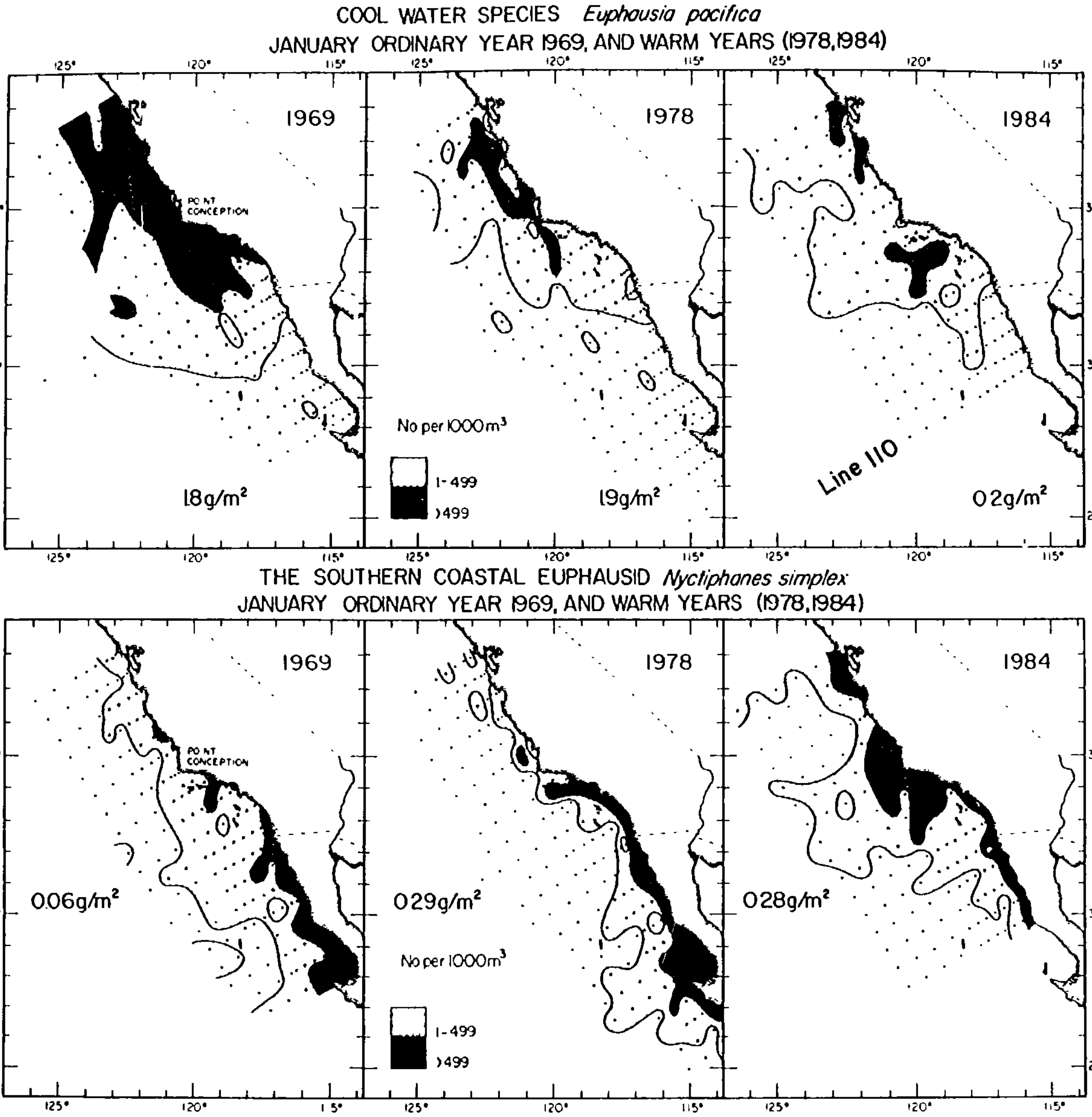


Fig. 3 Station by station proportions along, A. station line 90 off southern California of the northern, cool water euphausiid *Euphausia pacifica* and the southern, warm water species *Nyctiphanes simplex* and *Euphausia eximia*. B. cool January 1956 compared with C. warm 1984.

of the central water mass have been ignored. This is because they rarely contribute significantly to the California Current community. During the warm periods, temperatures in the offshore part of the current did not show increases relative to seasonal means. The eastward limit of their ranges lies along lines of fastest flow, well to the west of the coastal region in which warming was pronounced. Thus, species' range limits tend to lie along, not across, isolines of temperatures or steric height.

Mention must be made of distributions in a month other than January. In April, upwelling is often strongest, particularly off central California. Southward flow is then strenghened, compared with January. During warm Aprils of 1958 and 1984 *E.pacifica* extended southward into southern California waters, but little beyond (Fig.9). In the cool April of 1962 the range extended to 27°N off mid-Baja California, and biomass was twice that of the two warmer Aprils.

Conversely, *N.simplex* was well established



COOL WATER SPECIES *Euphausia pacifica*
JANUARY ORDINARY YEAR 1969, AND WARM YEARS (1978,1984)

THE SOUTHERN COASTAL EUPHAUSID *Nyctiphanes simplex*
JANUARY ORDINARY YEAR 1969, AND WARM YEARS (1978,1984)

Fig. 4 California Current distributions during January of northern (*Euphausia pacifica*) and southern (*Nyctiphanes simplex*) euphausiids. The ordinary year 1969 compared with the warm years 1978 and 1984. Average biomass values are indicated for the area of station line 110 northward.

off central and southern California in April of warm 1958 and 1985, but not in cool 1962 (Fig.9). Overall biomass was low in 1962, 0.01g/m^2 north of line 110 and 0.13g/m^2 when the full range to the south was included. This latter is still far lower than 3.98g/m^2 recorded for April 1984, which included new population centers in the southern California bight and Montery Bay (36°N).

An animal which is more passive and short-lived than the euphausiids, the typically offshore, warm-subtropical, pelagic tunicate *Doliolum denticulatum* examined by Berner & Reid (1961), showed little seasonal change in distribution during cool years, prior to 1957, thereby resembling the euphausiids. Seasonal

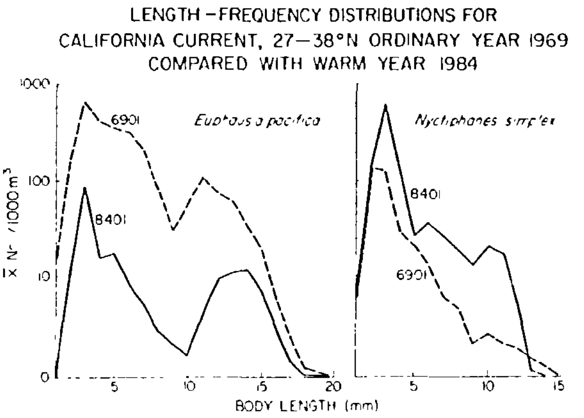


Fig. 5 Length frequency distributions for the California Current, ca. 29-38°N, for *E. pacifica* and *N. simplex*, ordinary year 1969 compared with warm 1984. (cf. Fig. 4).

temperature changes were interpreted as being of too short a term to bring about much distributional response. However, during the extended warm period of mid-1957 through 1959, this doliolid penetrated a previously cool part of the California Current north of Point Conception and thereby broadened its distribution to include much of the California coast. In 1984, this appears to have happened to the southern euphausiid *N. simplex*, but not to the Pacific central euphausiids.

We have seen that annual shifts in range limits, here, have been no more than about 200 to 400km. Seasonal shifts have been somewhat less. This extent of shift is of the same order shown by euphausiids which occupy even those systems where currents undergo seasonal reversal, as under monsoon regimes in the South China Sea (Brinton, 1975) and the Arabian Sea (Brinton & Gopalakrishnan, 1973). Like certain calanid copepods species which undergo diapause at depth during unfavorable conditions (Alldredge et al., 1984), many euphausiid species exploit a water column having a temperature range of 5 to 10°C, generally a greater span than is encountered across their ranges. Their capacity to orient vertically may then be used when upper-level temperature becomes unfavorable.

Thus, while showing conservative biological responses to recent variation in ocean climate, individual euphausiid species can locally undergo

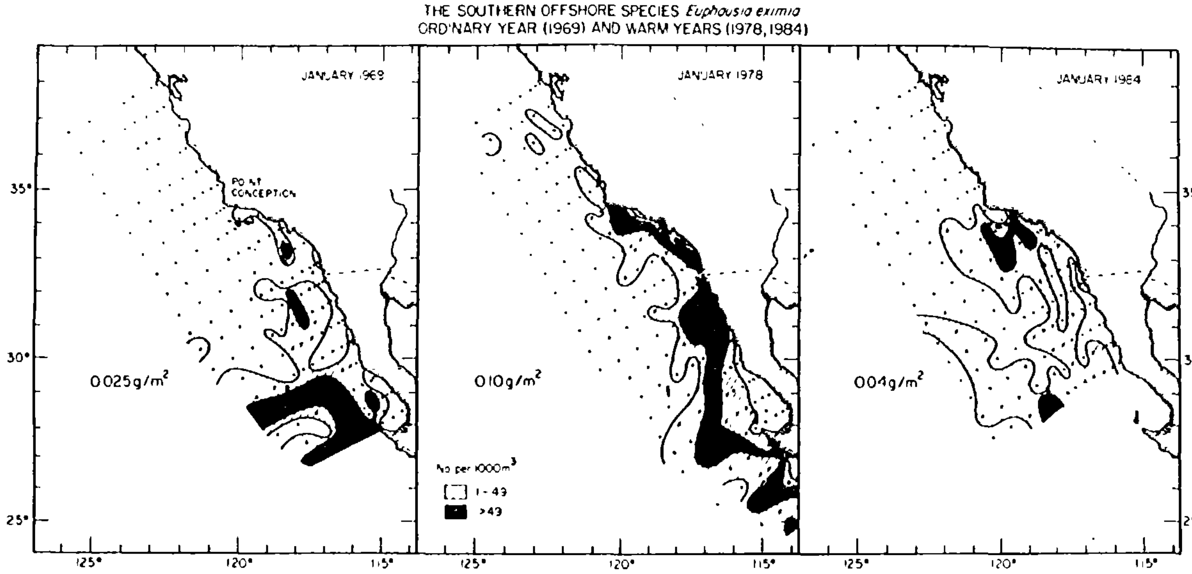


Fig. 6 California Current distributions and average biomass values for the southern euphausiid *Euphausia eximia*, ordinary year 1969 compared with warm 1978 and 1984.

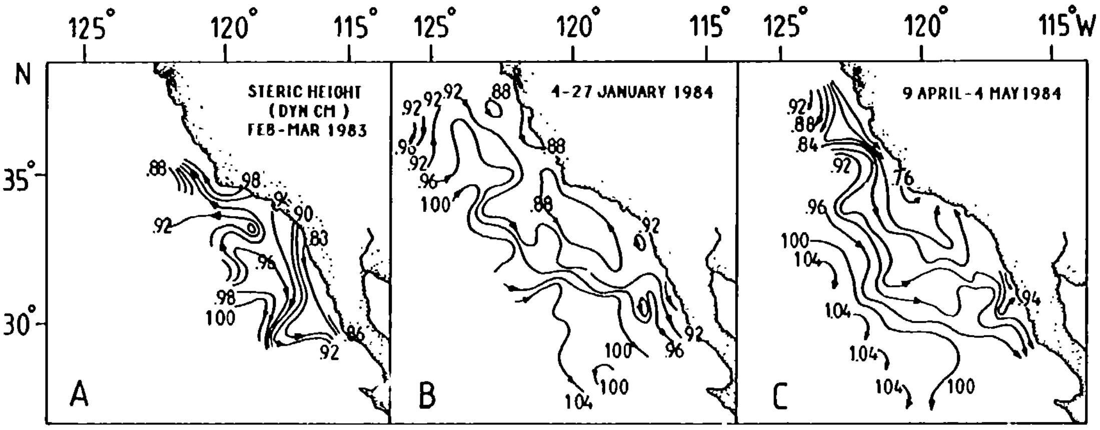


Fig. 7 Steric height 0/500 db in dynamic centimeters for, A. R/V Townsend Cromwell survey 8302-3 (Fig. 1 from Lynn, 1983). B. from 4-27 January 1984, C. for 9 April to 4 May 1984 (from Scripps Inst. Oceanogr. 1984a,b)

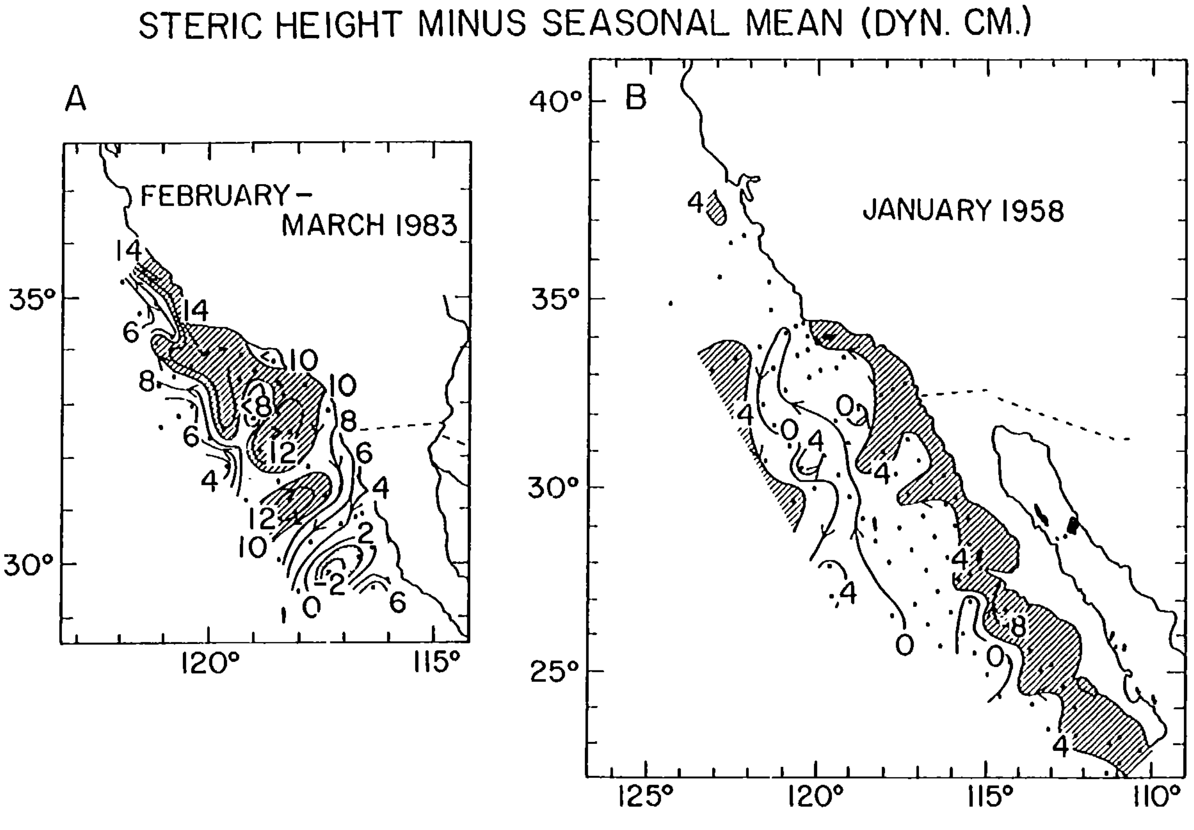
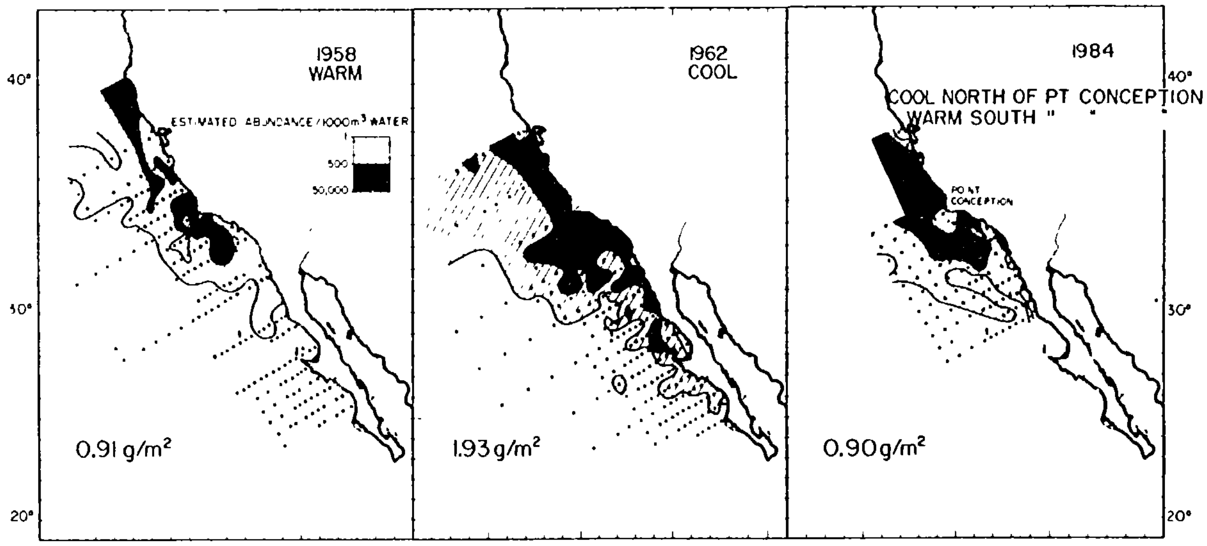


Fig. 8 The difference between steric height values and the seasonal mean values in dynamic centimeters. A. Feb.-March 1983 (Fig. 2 from Lynn, 1983). B. January, 1958.

APRIL
Euphausia pacifica



APRIL
Nyctiphanes simplex

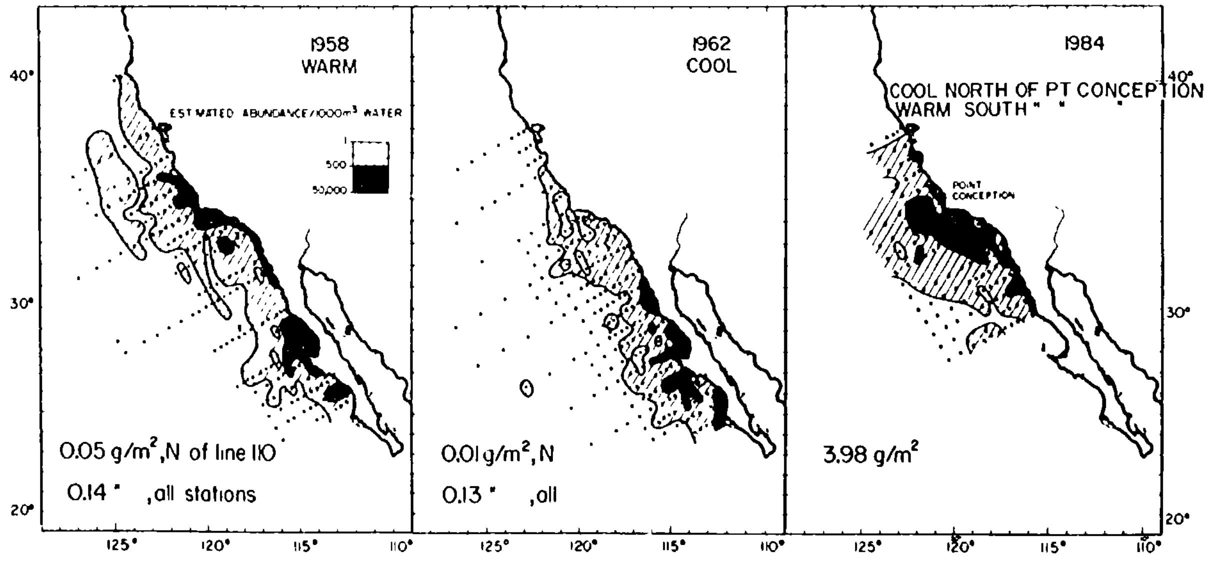


Fig. 9 California Current distributions during April 1958, 1962 and 1984 and average biomass values (Line 110 northward) for the southern euphausiid *Nyctiphanes simplex* and northern *Euphausia pacifica*.

five to ten fold interannual changes in biomass, with southern species dominating in warm times and northern species in cool times.

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THE GENETIC STRUCTURE OF ZOOPLANKTON POPULATIONS

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INTRODUCTION

Extensive biogeographic ranges are characteristics of zooplankton species (Van der Spoel & Heyman, 1983). Some oceanic species' distributions include both the Atlantic and Pacific Oceans and/or both hemispheres. However, an individual's dispersal capabilities may be limited relative to the species' range. Random interbreeding across the species is consequently either improbable or impossible, and it becomes useful to determine the extent and size of the "local populations" (i.e. groups of randomly interbreeding, conspecific individuals) that comprise the species. Restricted gene flow (reproductive isolation) among local populations may allow divergence in their genetic character, so that the species consists of a patchwork of genetically differentiated local populations. The division of the species into reproductively isolated, genetically differentiated sub-units is termed genetic structure.

Potential barriers to dispersal in terrestrial environments may be obvious, including mountain ranges, rivers, or habitat patchiness, and genetically structured species populations may be readily explainable. However, barriers to the dispersal of zooplankton in the open ocean are less evident. The most probable barriers for planktonic organisms are strong and persistent hydrographic features (e.g. fronts, pycnoclines, rings, gyres). However, the ability of individuals to cross water mass boundaries is unclear. Additionally, the distance an individual may travel and still be integrated into a new population (the maximum dispersal range) is difficult if not impossible to estimate for open ocean plankton. The degree to which populations may be reproductively isolated by simple distance is thus difficult to calculate. This question is theoretically interesting, but predictive hypotheses and quantitative solutions require estimates of migration rates among populations.

Given the subtle and changeable nature of potential barriers to gene flow in planktonic environments, it seems fruitless to attempt to exactly delimit the spatial extent and size of a local population of a zooplankton species. Rather, descriptions of structure must rely on statistical analyses of geographic patterns of genetic variability across a species' range.

I will briefly review here previous descriptions of genetic variability in zooplankton populations. Although breeding studies are mentioned, I have focussed this review on studies of biogeographic patterns of allozymic variability. Allozymes are forms of enzymes differing in electrophoretic mobility. Allozymic variability is presumed to reflect genetic differences (allelic variants of the encoding locus), but variability of enzymes with exogenous substrates may result from induction or other non-genetic processes (Gillespie & Kojima, 1968; Johnson, 1974). Geographic patterns of morphological variation may provide similar evidence of a genetically structured population, but morphological traits are presumably more strongly influenced by environmental conditions. Since allozymes are discrete, quantitative traits, they lend themselves well to statistical treatments.

STATISTICAL ANALYSES OF GENETIC STRUCTURE

Describing the genetic structure of zooplankton populations and inferring patterns of gene flow from spatio-temporal patterns of genetic variability is a somewhat intricate statistical problem. Tests of allozyme frequency heterogeneity, heterozygote deficiencies and measures of genetic distance are conventionally used as indicators of the degree of genetic differentiation among natural populations. Following these descriptions, it is useful to consider the relationship between genetic differentiation and geographic separation. The rate and smoothness in decay of genetic similarity of local populations separated by increasing distances may reveal the position of barriers to gene flow and, by comparing rates of decay for many taxa, suggest relative dispersal capabilities.

Traditionally, population genetic structure has been described using F-statistics based on the amount of inbreeding associated with partial reproductive isolation of local populations (Wright, 1951, 1965). Calculations of F-statistics for multiple loci (Nei, 1977) rely on comparisons between heterozygosity observed (the frequency of heterozygotes averaged across all loci) in individual and pooled collections and heterozygosity expected with random mating across all populations sampled (Levenee, 1949). Population structuring decreases heterozygosity, as described by the Wahlund Effect (Wahlund, 1928): $\overline{Aa} = 2\,\bar{p}\,\bar{q} - V_g$ (where V_g is the variance of the less common allele among local populations, and $\bar{p}$ and $\bar{q}$ are mean allele frequences for the pooled collections). Thus, heterozygote deficiencies across numerous loci are indicative of genetic structure (Wright, 1969).

Other statistical means of describing population genetic structure are based on comparisons of allozyme frequencies among all collections. As a first approximation, frequencies may be compared by a statistical test of heterogeneity, the G-test (Sokal & Rohlf, 1981). More powerful statistics have been developed specifically for genetic data, including an array of genetic distance measures. A frequently used distance measure *D* (Nei, 1972) has been used for a wide variety of taxa, and values have been approximately correlated with taxonomic separation (races, subspecies, species) (Thorpe, 1983).

An additional means of describing genetic structure is by comparison with predictions of theoretical models of gene flow. One of the simplest models of population genetic structure, and one that is appropriate to the planktonic environment, is the "stepping-stone" model of Kimura (1953), with quantitative analysis by Kimura & Weiss (1964). According to this model, correlation of allele frequencies among local populations in one-, two- or three-dimensional arrays (with isotropic migration between adjacent local populations) will decrease with distance between local populations at a rate dependent upon migration rate. The evidence presented above suggests that zooplankton exhibit two-dimensional arrays of partially isolated populations. If so, Kimura & Weiss (1964) predict that the correlation of allozyme frequencies among local populations will decay logarithmically. This prediction has not been widely tested, but a single study is discussed below.

CAUSES OF DIVERGENCE

The causes of genetic divergence of local populations are various, and include differential selection on local populations and genetic drift (the accumulation of random changes in genetic characters). The driving forces behind genetic differentiation and the relative contributions of selection and drift may be difficult or impossible to establish.

The magnitude of drift is a statistical function (derived from the expected variance in allele frequency) determined primarily by the size of the offspring generation, according to the function: $V_g = p\,q/2N$ (where V_g is the variance in allele frequency after one generation, p and q are the frequencies of the alternate alleles at a give locus, and N is the size of the offspring generation). For populations of 1000 or greater, drift is negligible regardless of allele frequencies. Bottlenecks and other events during which drift may strongly alter allele frequencies would seem unlikely for zooplankton populations, making them largely immune to random genetic fluctuations. There is, however, one situation when drift may be significant even for large populations. When individual contribution to recruitment is highly variable (as is typical of many invertebrate, including planktonic crustacea), the effective population size is very small (Wright, 1969) and V_g may be considerable regardless of the number of potentially reproductive individuals.

A second primary force driving genetic divergence of populations is selection. Differential selection in different portions of a species' range may result in regional differences in a species. It is unlikely that selection on a single enzyme locus might structure a species, and allozymic variability may be considered to track, not drive, differentiation. (For this reason, allozymes are frequently treated as selectively neutral and are regarded as "markers" of population phenomena). The selective neutrality of the traits used to describe population genetic structure is of considerable importance, since estimates of gene flow and migration may then be derived directly (Wright, 1969). Alternatively, the selection coefficients of non-neutral traits must be determined, which may be impossible. However, difficulties in establishing causes of differentiation do not interfere with description of population genetic structure.

EVIDENCE OF GENETIC STRUCTURE IN ZOOPLANKTON SPECIES

Studies of allozymic variation in zooplankton populations have demonstrated that plankton taxa are highly genetically variable, including copepods (Battaglia et al., 1978; Burton et al., 1979; Bucklin & Marcus, 1985) and euphausiids (Valentine & Ayala, 1976; Ayala & Valentine, 1979; Fevolden & Ayala, 1981; Bucklin & Wiebe, in the press). High variability provides numerous allozymic variants for potential indicators of genetic divergence.

Experimental studies of interbreeding of conspecific but distantly separated individuals have provided evidence of genetic differentiation. Laboratory crosses between eastern and western Atlantic conspecific individuals yielded viable offspring for four species of the harpactacoid copepod, *Tisbe*, but crosses between individuals of another species, *T. clodiensis*, produced no offspring (Battaglia & Volkmann-Rocco, 1973). Similarly, crosses between Atlantic and Pacific individuals of the calanoid copepod, *Acartia clausi*, were unproductive (Carillo et al., 1974). Clearly, what are now considered to be species are distinctly structured on the largest scale, and perhaps consist of distinct, geographically isolated species.

Studies of geographic variability of allozymic frequencies have also provided evidence of genetic structure in zooplankton populations. Subdivision of the species into local populations, which are only partially reproductively isolated and may correspond to distinct races, usually occurs on smaller geographic scales than the inter-ocean differences demonstrated by breeding experiments. Intertidal tide pool populations of the harpactacoid copepod, *Tigriopus californicus*, show strong differentiation (divergence of allozyme frequencies at several enzyme loci) among nearby pools (Burton et al., 1979; Burton & Feldman, 1981), indicating structuring on a very small geographic scale. Allozymic frequency differences also indicated racial differentiation of geographically distrinct populations of the copepods *Tisbe holothuriae, T. clodiensis and T. reticulata* in Mediterranean and N. Atlantic coastal waters (Battaglia & Bisol, 1975). Breeding studies confirmed some degree of differentiation among *T. reticulata* populations, since viability was reduced in crosses between individuals from different Mediterranean localities (Battaglia, 1957). Differentiation at the level of genetic races may be an adaptive response to environmental variation across a species' range.

Neritic copepod species are also genetically structured. The geographic scale of structuring is not known, but divergence has been demonstrated at the mesoscale (periodic variation on the order of weeks to months and tens to hundreds of km: Stommel, 1963). In a study of allozymic variation at loci encoding four enzymes in the calanoid copepod, *Labidocera aestiva*, the species was demonstrated to be highly genetically variable (Bucklin & Marcus, 1985). Further, samples collected in three regions from Cape Cod to Florida along the east coast of the U.S.A. exhibited significant genetic differentiation. First, there were almost fixed differences in allozyme frequencies at one enzyme locus, which were highly significant by a G-test (Sokal & Rohlf, 1981). Second, values of the statistic of genetic distance, *D* (Nei, 1972), averaged 0.20 ±

standard deviation of 0.08, reflecting divergence to at least reproductively isolated local populations (Ayala, 1975). And third, there were highly significant heterozygote deficiencies, compared to heterozygote frequences expected with random mating (Levene, 1949), at five loci. Differentiation at this scale may be best explained by geograpic separation resulting in isolation by distance (Wright, 1943). Gene flow among the three regions must be limited to allow genetic divergence of the populations. Genetic divergence may be driven by differential selection in the three regions along the species' extensive latitudinal range.

GENETIC STRUCTURE OF EUPHAUSIID POPULATIONS

Studies of patterns of allozymic variability in euphausiids, a prevalent planktonic taxon in coastal and oceanic waters, have also revealed evidence of genetic structure. Several species of *Euphausia* have been assayed for allozymic variability among populations: *E. distinguenda*, a tropical species, showed some differentiation between samples separated by three degrees latitude ($D = 0.056$) (Ayala & Valentine, 1979). Another species, *E. superba*, the large Antarctic species, exhibits little allozymic variability (Ayala et al., 1975; Fevolden & Ayala, 1981). Perhaps as a result of low variability, there were no differences in allozymic frequencies among several collections (Fevolden & Ayala, 1981), and thus no apparent genetic structuring.

Structuring of oceanic zooplankton populations suggests that hydrographic features (such as eddies, fronts or current boundaries), geographic distance or other biological or physical phenomena may prevent random interbreeding across planktonic species. Determination of the scale of structuring will require appropriately designed sampling programs.

Outlines of the results and conclusions of two descriptions of the genetic structure of euphausiid populations follow. These are attempts to determine the spatial and temporal scale of genetic structure in zooplankton populations and to examine theoretical predictions of gene flow using allozymic data.

EUPHAUSIIDS OF THE NORTH ATLANTIC SLOPE WATER

Allozymic analysis of seven samples of the euphausiids, *Euphausia krohnii* and *Nematoscelis megalops*, collected between October 1981 and October 1982 in a 300 by 700 km area of the western North Atlantic Slope water revealed high level of genetic variability (Bucklin & Wiebe, in the press). Based on data from eight loci encoding five enzymes, both species were highly polymorphic and heterozygous. Allozymic frequencies differed significantly among the seven collections by the G-test (Sokal & Rohlf, 1981), indicating significant heterogeneity of successive samples of each species [$G_{H(132)} = 791.5$ for *E. krohnii* and $G_{H(125)} = 563.8$ for *N. megalops*, $P < 0.001$ for both]. Genetic distances (D, Nei, 1972) among samples of each species were typical of distances between local populations (mean D between samples of *E. krohnii* was $D = 0.116 \pm 0.112$ and between samples of *N. megalops* $D = 0.203 \pm 0.073$). Intraspecific genetic distances were not the result of sampling error: spurious genetic distance from sampling error (D_s, Nei, 1973) was $D_s = 0.037$ for *E. krohnii* and 0.032 for *N. megalops*.

The sampling pattern unfortunately does not allow discrimination of spatial and temporal causes of genetic divergence of conspecific populations. Allozymic frequencies varied randomly among the seven collections of each species (Fig. 1).

Random variation may be explained by spatial patchiness in both species populations, by temporal fluctuations in the genetic character of the populations, or both.

EUPHAUSIA PACIFICA IN THE CALIFORNIA CURRENT

The euphausiid, *Euphausia pacifica*, is frequently the most abundant euphausiid of the California Current, as well as the predominant zooplankter in terms of biomass (Brinton, 1962).

Dense aggregations, which may correspond to local populations, occur in submarine canyons along the California coast. Recruitment is tied to

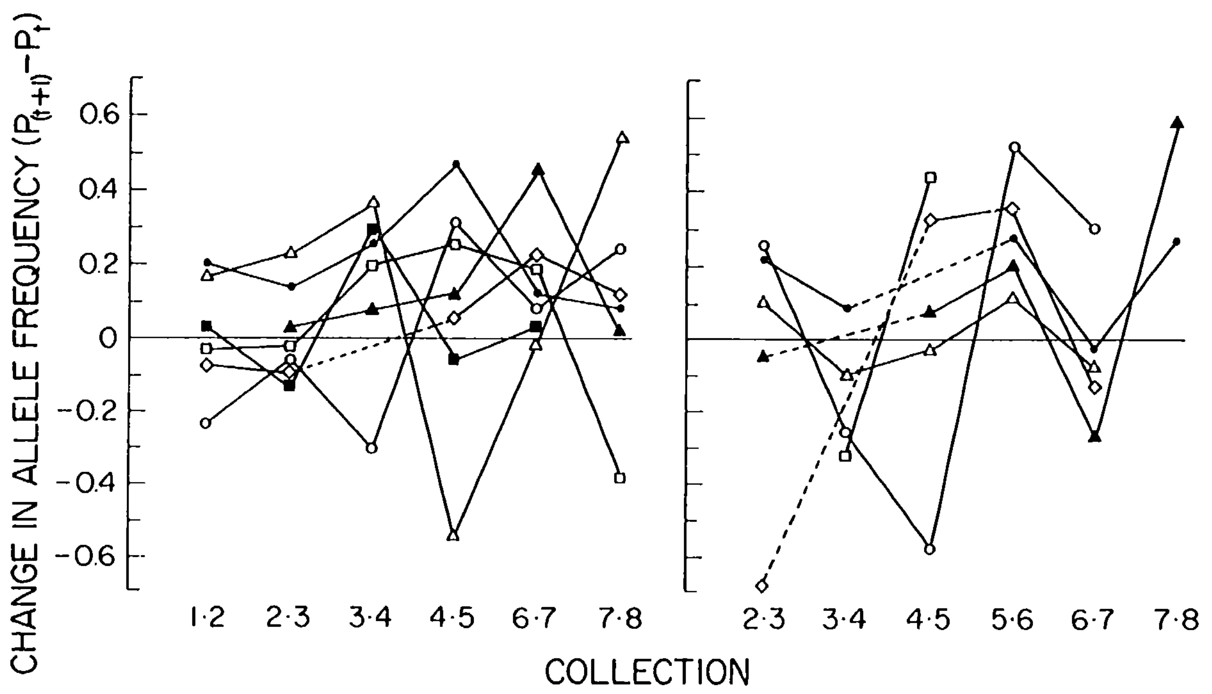

Fig. 1 Differences in frequencies of the most common allozyme (allele) of each locus between successive collections of the euphausiids, *Euphausia krohnii* and *Nematuscelis megalops,* from the western North Atlantic Slope Water. Seven collections were made in 1981 and 1982, with an additional collection in August, 1984. Allozyme frequency changes at each enzyme locus for successive samples were calculated as $p_{(t+1)} - p_{(t)}$, where p is the allozyme frequency in each sample, and t is the sample number. Collection date corresponding to each number are: 1) 27 October 1981, 2) 24 November 1981, 3) 12 December 1981, 4) 15 December 1981, 5) 8 February 1981, 6) 16 August 1981, 7) 5/6 October 1982, 8)10/11 August 1984. Numbers along the abcissa indicate allozyme frequency changes between samples 1 and 2, etc. Missing sample numbers indicate absence of the species from that collection.

upwelling intensity and is apparently local, with multiple centers of recruitment along the California coast (Brinton, 1976). The persistence and geographic stability of aggregations suggests that the species might be genetically structured.

Samples of *Euphausia pacifica* were collected along a north-south transect from just north of Point Conception to San Diego in October 1984.

Collections at six sites were made in association with the California Cooperative Fisheries Investigations (CalCOFI), which samples a grid of stations quarterly. Eight of nine loci encoding eight enzymes assayed for allozymic variability were polymorphic. Genetic distances were calculated for pairwise comparisons among all collections by techniques of Nei (1972). *D* values averaged 0.175 ± standard deviation of 0.107. This reflects significant genetic differentiation of samples collected over a short geographic range. Clearly the species is genetically structured, and it now becomes interesting to look for statistical relationships between allozymic frequencies and geographic separation. Decrease in the correlation of allozyme frequencies between samples over distance was determined as a test of predictions of the stepping-stone model of gene flow (Kimura, 1952; Kimura & Weiss, 1964). The decrease in correlation was approximately logarithmic with distance ($r = -0.77$, $P<0.05$) (Fig. 2), suggesting that *E. pacifica* local populations approximate a two-dimensional array with isotropic migration between adjacent populations.

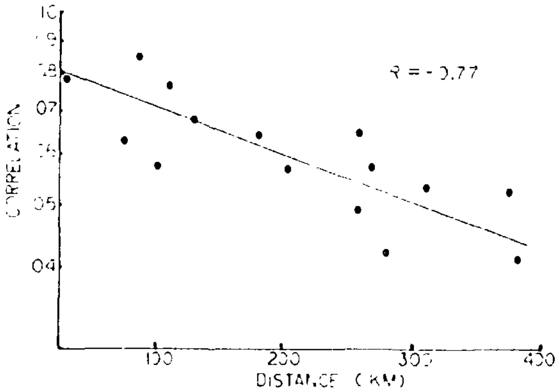

Fig. 2 Regression analysis of allozymic variability of the euphausiid, *Euphausia pacifica,* in six samples collected along a 400km north-south transect in the California Current. The value of the correlation coefficient for each comparison of allozyme frequencies in two samples is graphed against distance separating the collection sites. The line is the function best fitting the data (r= -0.77, P<0.05). Such a logarithmic relationship conforms to the theoretical expectations of Kimura & Weiss (1964) for genetic structuring of a species distributed as a two-dimensional array of local populations with isotropic migration between adjacent populations.

CONCLUSION

Although causes of differentiation cannot be determined, the allozymic data indicate that zooplankton species may be structured on small spatial and temporal scales. Evidence of genetic structuring of nearly all of the species studied suggests that panmixis across zooplankton species is not usual. The most important conclusion from these studies is that the genetic homogeneity of zooplankton populations over even short distances cannot be assumed. There may be barriers to dispersal in plankton environments, including physical or hydrographic features, biological differences among conspecific populations, or geographic distances between populations may be too great to be spanned by individual dispersal. Any or all of these factors may result in restricted gene flow among conspecific populations, and give rise to genetically structured species populations.

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SIMILARITY OF PLANKTON DISTRIBUTION PATTERNS IN TWO NEARLY LAND-LOCKED SEAS: THE MEDITERRANEAN AND THE RED SEA.

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INTRODUCTION

Although the plankton populating the Red Sea has not been studied as thoroughly as that of the Mediterranean, numerous similarities have been pointed out between them. Indeed there are strong analogies between the physical and hydrological conditions prevailing in these two seas. The Mediterranean is connected to the Atlantic by a narrow strait about 300m deep. Rapid evaporation in the Eastern basin whose southeastern shore is a desert results in a deficit which is not offset by river drainage and leads to an inflow of water from the Atlantic. In the Mediterranean, salinity is about 36 ^{o}/oo in the Strait of Gibraltar and registers a progressive easterly increase to about 37 ^{o}/oo off Tunisia and 38 ^{o}/oo at the latitude of Naples. Below 300m, salinity and temperature are constant at 39 ^{o}/oo and 13°C respectively. Salinities and temperatures are slightly higher in the Eastern Basin. The outflow of these deep waters forms the Lusitanian current in the Northeast Atlantic.

The smaller Red Sea is connected to the Indian Ocean by a shallow (100m) sill. It consists of a long narrow basin lying between two arid, tropical land masses. Evaporation is thus great and salinity is high especially in the northern part. Surface currents depend on monsoon winds south of 20°N (Morcos, 1970). During the winter months, these winds blow south south-easterly and push superficial waters north from the Gulf of Aden. As the water moves northward, its salinity increases from 36 to 41 ^{o}/oo in the north. In the south, deep waters flow out into the Indian Ocean. In May, the wind reverses and blows north northwesterly until September. So both the superficial waters and the deep waters flow out of the Red Sea balanced by an inflow of water at intermediate depths. At depths greater than 200m, salinities and temperatures stay around 41 ^{o}/oo and 22°C respectively.

Given their physical similarities, it is not surprising to find parallel similarities in the patterns of plankton distribution. This report focuses on comparison of four aspects of these biological processes: quantitative, geographical and bathymetric distributions and faunistic relations with adjacent oceans.

QUANTITATIVE DISTRIBUTION

Jespersen (1923) published the first comprehensive study on Mediterranean plankton based on samples collected during the Danish cruises. He showed that planktonic standing crops steadily dwindle from west to east: Bay of Cadiz (Atlantic), Alboran Sea, central sector of the Western Basin, Tyrrhenian Sea and Eastern Basin.

The only exceptions to this pattern are the enriched zones at the mouths of rivers (Gulf of Lion, north part of the Adriatic Sea) and the Ligurian divergence. The main reason for this pattern is a shortage of nutrients, especially phosphates (Sournia, 1973) even in the deep water.

Thus, ascending currents, divergences and upwelling do not enhance surface nutrient concentrations, except in the Alboran Sea and off the North African coast where the Atlantic inflow has relatively high nutrient concentrations. Gaudy (1985), however, recently showed that the temperate waters of the Atlantic were not significantly richer in plankton than those of the Mediterranean, even in the Eastern Basin.

Measurements made in the Red Sea suggest a similar situation. In a recent report, based on a series of hauls extending from the Gulf of Aden to the centre of the Red Sea, Beckmann (1984) noted an overall decrease in plankton from south to north except in the shallow waters overlying the Hanish Sill where mixing of pelagic and neritic communities resulted in exceptionally high concentrations.

In both seas the biomass of plankton decreases rapidly with depth below 200 to 300m, as observed by Greze (1963) in the Ionian Sea and Weikert (1982) in the centre of the Red Sea.

GEOGRAPHIC DISTRIBUTION OF ORGANISMS

Geographical distributions are better documented for the Mediterranean. The influx of Atlantic species into the southwest of the Western Basin was recorded long ago, notably through the presence of the euphausiid *Thysanoessa gregaria* and the siphonophore *Diphyes dispar* (Ruud, 1936; Bigelow & Sears, 1937).

Accurate data concerning the distribution of numerous plankton species are available (pteropods, chaetognaths, euphausiaceans and decapods crustaceans) for the Mediterranean Sea. For all groups, distributions can be classified into four similar categories; for example, in chaetognaths (Fig. 1), Furnestin (1970) described: 1. "Ubiquitous" species, present in all sectors (e.g. *Sagitta enflata),* 2. "Atlantic" species, found along the axis of the inflowing oceanic waters (e.g. *Pterosagitta draco* which can be found in the Alboran Sea and off the North African and Italian coasts to a latitude of Naples), 3. "Oriental" species, abundant not only in the eastern part of the Mediterranean Basin but also in the Tyrrhenian Sea which is fed by the warmer and saltier waters from the east. They are rare west of a line through Corsica and Sardinia which constitutes the border between the Eastern and Western Mediterranean water (e.g. *Sagitta serratodentata)* and 4. "Boreal" species, namely *Sagitta setosa* whose southernmost limit in the northeast Atlantic is the Bay of Biscay. This boreal relict is abundant throughout the northern sectors of the Mediterranean where the waters have low salinities and temperatures i.e. Gulf of Lion, Ligurian Sea, Adriatic Sea, Aegean Sea and in the Black Sea.

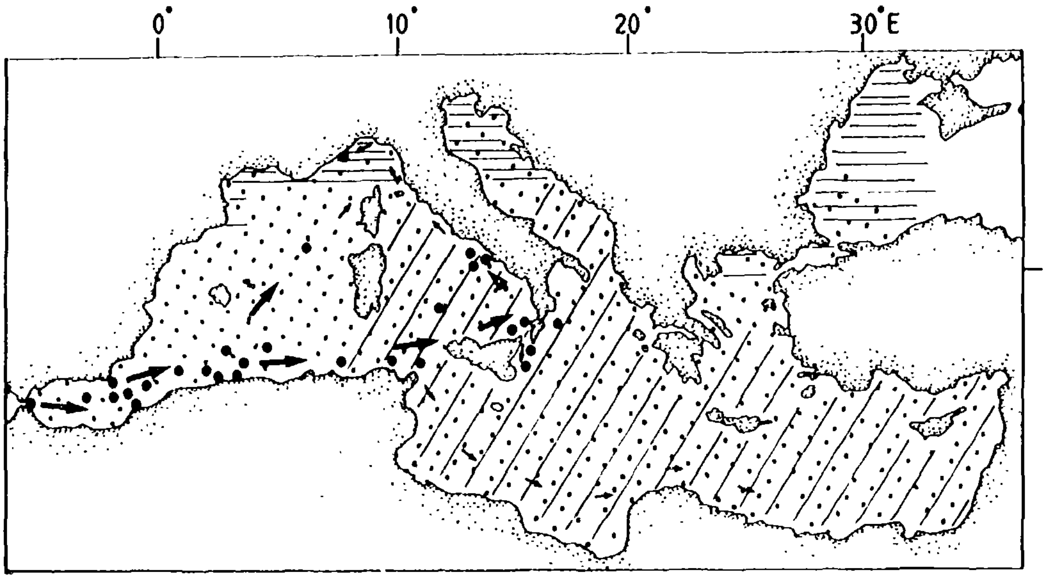
For the southern waters of the Red Sea several authors have reported the occurence of many immigrant species from the Gulf of Aden (in Halim, 1969), and Beckmann (1984) correlated the seasonal presence of copepods such as *Eucalanus* with influxes of oceanic water.

The first data on the distribution of an entire planktonic group throughout the Red Sea were for chaetognaths (Casanova, 1984). Apart from the absence of a boreal group, the distributions of the chaetognath species in the Red Sea can be categorised similarly to those of the Mediterranean (Fig. 1): 1. "Ubiquitous" species, present throughout, from the Strait of Bab-el-Mandeb to the Gulfs of Suez and Aqaba (e.g. *Sagitta enflata),* 2. "Meridional" species which live in the superficial layer of the southern quarter of the Red Sea where the oceanic influence maintains salinity at or below 38 $^{o}/oo$ (e.g. *Pterosagitta draco),* and 3. "Septentrional" species, halophilic species which thrive where salinity is 38 to >41 $^{o}/oo$ in the sectors north of 17-18°N (e.g. *Sagitta pacifica).*

Thus, both seas have "ubiquitous" species; halophilic species with the "oriental" species of the Mediterranean corresponding to the "septentrional" species of the Red Sea and oceanic species with the "Atlantic" species in the Mediterranean and the "meridional" species in the Red Sea indicating the penetration of oceanic waters. These oceanic species may be represented by either permanent or transient populations in areas where the influence of oceanic inflow is the greatest. However, the specific composition of the plankton of these two seas is very different since the Mediterranean fauna originates from the Atlantic and the Red Sea fauna from the Indian Ocean.

DEEP WATER PLANKTON

In both seas, the deep water plankton is much sparser than in the adjacent oceans. The most probable explanation for this is the effects of the very warm deep temperatures. In the Red Sea, where the deep water temperatures are 22°C, Wishner (1980) claims that most of the available food is decomposed before it reaches the bottom; furthermore oxygen content is abnormally low. In



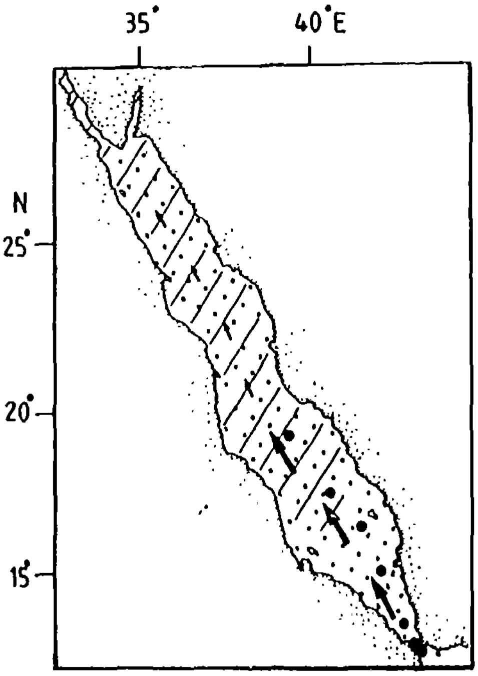


Fig. 1. Distribution of some chaetognaths illustrating the four categories of distribution pattern. Boreal: *Sagitta setosa* (Mediterranean only); ubiquitous: *S. enflata;* halophilic: *S. serratodentata* (Mediterranean) and *S. pacifica* (Red Sea); oceanic: *Pterosagitta draco*. Oceanic water currents are indicated by arrows.

addition, at these temperatures, the metabolism of the organisms is rapid and so their food requirements are higher. Nevertheless, in the Mediterranean there are a few bathypelagic species such as the scyphomedusan *Periphylla periphylla*, the mysidacean *Eucopia hanseni* and the decapod crustacean *Gennadas elegans*, but none of these occur in the Red Sea. *Sagitta lyra*, a meso-bathypelagic chaetognath species, lives in the Mediterranean but not in the Red Sea, although it inhabits the Gulf of Aden where it may occur as shallow as 200m.

The shallow sills at Gibraltar (300m) and Hanish (100m) may be a barrier to the spread of many purely bathypelagic species (e.g. *Eukrohnia* spp.), but many species do gain access to the Mediterranean at some time in their lifecycle during ontogenetic, seasonal or diel vertical migration and the real barrier is the change in hydrology (Casanova, 1977). For example, the chaetognath *Sagitta planctonis* is meso-bathypelagic in the Bay of Cadiz, but a few specimens, usually young, can be carried in by the Atlantic current during their diel migrations. Once inside the Mediterranean, they are restricted to the stream of Atlantic water (0-300m) and being unable to migrate back down to their normal bathymetric level they disappear quickly (Furnestin, 1970). This poses the problem of the fate of those oceanic organisms carried into either the Mediterranean or the Red Sea.

FAUNISTIC RELATIONS WITH ADJACENT OCEANS

It has been known for some time that certain species cannot survive in these nearly land-locked seas. Ruud (1936) claimed this to be the case for *Thysanoessa gregaria* in the Mediterranean and Stubbings (1938) correllated the numerous shells of pteropods on the southern floor of the Red Sea to their death after entering the Erythrean zone. Recently, Beckmann (1984) described the sequence of changes ending in death which occur in the Copepod *Eucalanus crassus* as it is carried into the Red Sea via the Strait of Bab-el-Mandeb.

Thus oceanic species advected into the Mediterranean or the Red Sea disappear more or less rapidly the farther they are carried in from the ocean, depending on the varying strictness in their ecological requirements, but it is generally thought that in time the stock of species able to adapt to conditions in these seas will become increasingly richer because of the continual influx of animals from the ocean.

However, there are morphological differences between Atlantic and Mediterranean populations in thecosomes (Rampal, 1975) and decapod crustaceans (Casanova, 1977), and no specimens with intermediate characteristics have been observed in the vicinity of Gibraltar where the oceanic and mediterranean populations intermingle, thus they appear to interact as separate species.

Likewise, the amount of eye growth undergone by the Red Sea population of the chaetognath *Sagitta decipiens* by sexual maturity is much greater than its counterpart in the Gulf of Aden (Casanova, unpubl.); this difference would not persist if there was free gene flow through the Strait. Similarly Beckmann (1984) concluded from samples collected at a line of stations running from the Gulf of Aden to the middle of the Red Sea that the copepod *Haloptilus longicornis* is a species rare in the Strait of Bab-el-Mandeb; according to his data, it is a "septentrional" species with populations from the Gulf of Aden and from the Red Sea avoiding the Strait.

CONCLUDING REMARKS

Thus faunistic exchanges between the Atlantic Ocean and Mediterranean Sea, and the Indian Ocean and Red Sea appear only temporarily to enhance the populations close to the straits. Such exchanges do not have lasting effects since the new immigrants neither survive nor interbreed with the local population, at least for truly open-ocean species. Two lines of profitable lines of research can be suggested:

1. the study of copepods species occuring on both sides of the straits to investigate if there are morphological differences in tegumentary organs between the populations (cf. Fleminger, 1973).
2. assessment of the rate at which speciation has taken place in the different species and plankton groups, using thecosome shells (e.g. 12.000 years for *Cavolinia inflexa* in the Western Mediterranean) to date the appearance of present day species.

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THE DEMOGRAPHIC AND EVOLUTIONARY CONSEQUENCES OF PLANKTONIC DEVELOPMENT

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INTRODUCTION

Over half of all marine invertebrate species have incorporated a planktonic larval stage into an otherwise benthic life cycle (Thorson, 1950). The biogeographic implications of this life history pattern are profound (e.g. Scheltema, 1978; Jablonski & Lutz, 1983). Species with long planktonic larval stages tend to have greater geographical ranges and longer geological durations than those with restricted larval duration (e.g. Scheltema, 1978; Jablonski, 1982 for data on gastropods). The relation of dispersal and gene flow also has important implications for patterns of local adaptation and speciation (Scheltema, 1978). Hansen (1983), for example, finds that tropical neogastropods with non-planktotrophic development have exhibited greater speciation rates than those with planktotrophic development, presumably because the greater dispersal abilities of the latter make geographical isolation more difficult.

There is both inter- and intra-specific variation in planktonic development. This variation raises the question of the selective factors that favor the incorporation of planktonic stages in an otherwise benthic life cycle, and whether those factors can explain geographical (e.g. the rarity of planktonic larvae in the Arctic) and environmental (e.g. the rarity of planktonic larvae in the deep sea) patterns?

This paper reviews three types of models which have been or could be used to investigate the adaptive value of planktonic larval stages:

1. demographic trade-off models which assume the existence of negative correlations between the number of offspring produced and some measure of their size or provisioning,
2. niche shift models based on differential habitat utilization by larvae and adults, and
3. dispersal models based on the contribution of dispersal to fitness.

DEMOGRAPHIC TRADE-OFF MODELS

Models based on demographic trade-offs have been studied by Vance (1973), Pechenik (1979), Caswell (1981), Christiansen & Fenchel (1979), and others. The approach is to describe some portion of the life cycle, to derive from it a measure of fitness, to evaluate the sensitivity of fitness to changes in planktonic development, and to conjecture that those changes which increase fitness will be those observed in nature. The predictions of such models depend critically on the choice of a measure of fitness and on the inter-trait correlation pattern (Caswell, 1981).

For example, consider the allocation of resources to larval provisioning. This problem was examined by Vance (1973) as a way to distinguish planktotrophic (i.e. low level of provisioning) and lecithotrophic (i.e. high level of provisioning) feeding behaviours. Assume that total development time T is fixed; it is partitioned into a non-feeding (e.g. lecithotrophic) stage of duration x and a feeding stage of duration T-x. The greater the degree of provisioning of the larva, the larger the value of x. The probabilities P_1 and P_2 of surviving the two stages are given by:

$$P_1 = \exp(-\mu_1 x)$$

$$P_2 = \exp[-\mu_2(T-x)]$$

where μ_1 and μ_2 are the mortality rates in the two stages. The probability of surviving to settlement is then $\varphi = P_1P_2$. Assume that there is some negative correlation between offspring number (F) and provisioning (i.e. the more energy invested per offspring, the fewer of them can be produced). This produces a cost function relating F and x (Fig. 1).

Take as a measure of fitness (W) the expected number of offspring surviving to settlement: $W = FP_1P_2 = F\varphi$. This assumes that x does not affect the life cycle after settlement. Then the selective pressure on x is given

$$\partial W/\partial x = \varphi(x)\,[F'(x) - (\mu_1-\mu_2)\,F(x)]$$

The maxima and minima of W occur when $F'(x) = (\mu_1-\mu_2)F(x)$, at which point $\partial W/\partial x=0$. When F(x) is concave dowward [$F''(x)<0$], a stable maximum of W exists, with the optimal value of x varying directly with $(\mu_2-\mu_1)$ (Fig. 1a). In this case, one would expect to find "mixed" life histories, with a planktotrophic, feeding stage following a lecithotrophic stage supported by parental investment. On an interspecific basis, one would expect a continuous spectrum of life history types. On the other hand, when F(x) is concave upward [i.e. when $F''(x)$ is sufficiently greater then zero], as in Vance (1973); see Caswell (1981), only the extreme values of x are stable (Fig. 1b). In this case, only the extreme life history types are stable, and one expects to see planktotrophic and lecithotrophic life cycles as discrete alternatives. In both cases, the relative mortalities in the two stages are important in determining the optimal strategy, but must be evaluated in relation to the constraint function.

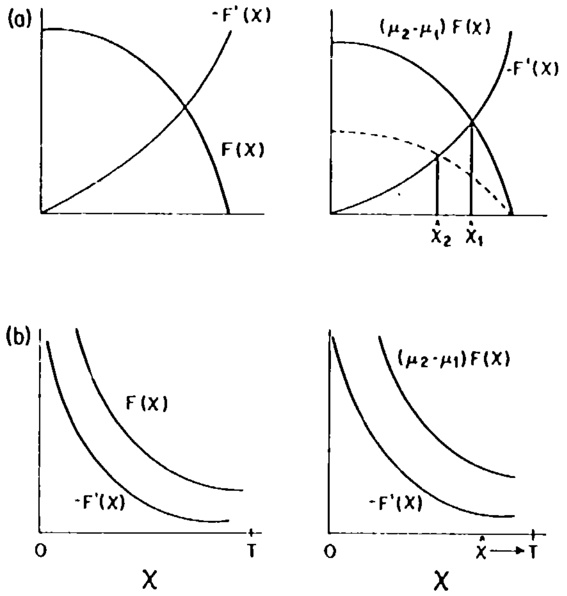

Fig. 1a Left: a concave downward cost function relating fecundity (F) and the duration (x) of the first stage (e.g.) lecithotrophic of a larval life cycle. Right: the intersection of -F' (x) and $(\mu_2-\mu_1)$ F(x) defines the optimal value of x indicated by $\hat{x}_1$. Decreasing μ_2 or increasing μ_1 to produce the dashed curve changes the optimal value of x to $\hat{x}_2$. That is, as planktotrophic mortality decreases or lecithotrophic mortality increases, the optimal life history spends less time in the lecithotrophic stage.

1b Left: As in Fig. 1a, but now the cost function is concave upward. Right: As drawn in this example, $(\mu_2-\mu_1)$ F(x) is always greater than -F'(x). As a result, selection leads to an optimal value of x at the extreme x = T, producing a life cycle without the second stage. If $(\mu_2-\mu_1)$ F(x) <-F'(x), selection results in x = 0, and the first stage disappears. Given such a cost function, mixed life cycles are not possible.

NICHE SHIFT MODELS

Many species, including those under discussion here, utilize two distinct niches during their ontogeny. Istock (1967)(cf. Slade & Wasserburg, 1975; Wilbur, 1980; Istock, 1984) introduced the first model to consider the effects of shifts from one niche to another during development. However, this model incorporates little of the biology of the species in the two habitats, and is based on questionable assumptions (to me, at least) about the action of selection.

A recent and very promising approach is that of Werner & Gilliam (1984)(see Gilliam, 1982; Werner, 1986). Their work is directly concerned with fish and amphibian life cycles, but has great potential application to marine invertebrates. They consider a life cycle passing through two or more distinct habitats. Each habitat is characterized by two curves, which give the growth rate [g(x)] and mortality rates [μ(x)] as functions of size (x). The overall fitness (the intrinsic rate of increase) depends on the size at which the individual switches from one habitat to another. Depending on the details, it might be advantageous to sacrifice potential rapid growth in a habitat with high mortality, or vice-versa.

Gilliam (1982) shows that, for populations near equilibrium, and in which metamorphosis occurs before sexual maturity, fitness is maximized by choosing the habitat which, at every size x, minimizes the ratio $\mu(x)/g(x)$. If mortality is uniformly lower and growth higher in one habitat than the other, only that habitat should be utilized. If one habitat has a higher mortality rate but also supports faster growth, the shapes of the growth and mortality functions can mandate a transition from one to the other at a particular size. This model is a promising approach to transitions which reflect trade-offs between growth rate and mortality, and should be investigated in the context of planktonic larval stages.

DISPERSAL MODELS

One obvious consequence of planktonic development is dispersal. However, neither of the models considered so far has explicitly included the possible benefits of having offspring settle in *different locations from parents.*

The analysis of dispersal strategies is complicated because the benefits of any given strategy are frequency dependent, i.e. they depend on the strategies adopted by the rest of the population. For example, suppose that a fraction D of offspring disperse, while 1-D do not. If a whole population has adopted a sedentary strategy ($D=0$), a mutant with $D>0$ will be able to invade, since it takes advantage of locations which the sedentary strategy leaves vacant. On the other hand, a mutant with $D<1$ can invade a population in which $D=1$, because the types which disperse all their offspring leave behind vacant sites in which a more sedentary type can flourish. An evolutionarily stable strategy (ESS) is one which, once adopted by the population, is proof against invasion by other strategies. It may not be "best" in the sense of maximizing any measure of fitness, but it is the strategy which is expected to result from selection.

Hamilton & May (1977), Comins et al. (1980), and Levin et al. (1984) analyze ESS's for dispersal in detail. The models are too complex to discuss here, but their conclusions point to two different situations which favour dispersal.

Scenario 1. Consider an environment composed of many sites, varying in time and space because of abiotic variation and local differences in density. Levin et al. (1984) have shown that the ESS for the fraction of offspring dispersed (D) in such situations increases with the probability of surviving dispersal (α); D goes to one as α goes to one. Thus, if there were no cost to dispersal, the ESS is to disperse all offspring. For small values of α, on the other hand, the ESS depends on the probability of extermination of local populations. Unless this probability is zero, the ESS for D is positive (and usually quite large) even as α goes to zero. Thus, given spatial variation and the chance of local extinction, some degree of dispersal is always favored.

Scenario 2. That environmental heterogeneity can lead to selection for dispersal is not surprising. Hamilton & May (1977) and Comins et al. (1980), however, show that dispersal is favoured even in a homogeneous environment. They assume a large set of identical patches, each supporting a limited number of adults. The undispersed offspring of the local adults and the offspring which settle in the patch compete for the space in each generation. A sedentary strategy is not an ESS because an invading strategy with $D>0$ decreases its competition with itself and increases that with the sedentary strategy by dispersal. As long as stochastic settlement patterns generate inter-patch variance in genetic composition, there is an advantage to dispersal.

CONCLUSIONS

Each of these classes of models predicts the evolution of planktonic larval stages under some circumstances. However, each does so for a different reason; the trade-off between offspring number and provisioning, the trade-off between planktonic and benthic growth and mortality rates and the advantages of dispersal in spreading the competition for adult sites. Given the multiplicity of potential causes revealed by the models, it seems unlikely that any single factor actually determines the evolution of planktonic life cycles in nature. The serious consideration of more general models, including those developed by population biologists concerned with other types of organisms, would probably make a major contribution to understanding planktonic life cycles.

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ESTUARIES AS TRANSITIONAL ZONES WITH REFERENCE TO PLANKTON IN THE NEAR SHORE WATERS

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INTRODUCTION

The present investigation was carried out from November 1981 to June 1982 in one of the big river estuaries in south India (17°20' - 18°00'N & 81°31' - 82°20'E), the Godavari estuary, a normal type estuary in which due to river discharge salinities are reduced as one goes upstream (Emery & Stevenson, 1957). It receives rain during SW and NE monsoons. The maximum rate of discharge is about one and a half million cubic feet per second. It has three main branches namely, Gautami, Vasista and Vainateyam and has extensive backwaters with dense mangrove vegetation near their outlets into the Bay of Bengal. Broadly three periods of water condition can be distinguished: the SW monsoon period from July to September, during which the entire estuary is freshwater: a postmonsoon period from October-January when there is considerable sea water penetration into the estuary establishing clear vertical stratification of the water column and a premonsoon period from February to June when typical marine features predominate and saline waters extend to 44 km above the mouth. In this latter period the upper reaches of the river dry up due to lack of freshwater flow.

METHODS

The Godavari estuary has a semidiurnal tidal cycle. The maximum range of tidal oscillation is 1.5m. In the entire stretch of 44km of the estuarine area three stations were set for periodic plankton sampling: station I, located near the mouth where the width of the river was 650m and the depth about 13m: station II, situated about 19 km from the mouth where the width was 1400m and about 10m depth: station III at the extreme end of the brackish water zone, about 44 km from the mouth. The width of the river was 900m and the depth about 10m. Plankton sampling and determination of the surface temperature and salinity were conducted during the day twice a month. A conical net, (50cm diameter) and 143µm in mesh size, was towed vertically from a depth of about 5m. The displacement volumes were measured and the abundance of the major zooplankton species was estimated (Fig. 1).

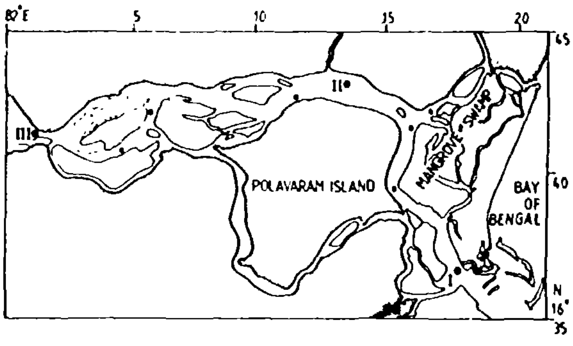

Fig. 1 Godavari Estuary with station locations

TEMPERATURE

Monthly mean temperature variations in surface water at station I ranged from 25°C in January to a maximum of 32.2°C recorded in May. The temperatures were always highest between 14.00 and 15.00 hours, indicating the variation was caused by diel irradiation, not by tides (Table 1A).

SALINITY

The variation in salinity was governed by the effect of tide and precipitation. During the monsoon period when the river is in spate the entire estuarine area was fresh and highly turbid. Tongues of saline waters could be detected only after October at station I, when penetration intensifies and extends further into the upstream area. At the head of the estuary, saline waters

Table I Monthly variations in the Godavari Estuary

A. Monthly mean surface temperatures (°C)								
	Nov.	**Dec.**	**Jan.**	**Feb.**	**Mar.**	**Apr.**	**May**	**June**
Station I	25.80	25.50	25.00	26.20	29.80	30.30	32.20	31.50
Station II	26.70	25.43	25.16	26.32	28.96	30.93	32.10	31.00
Station III	25.00	25.80	26.10	27.80	30.00	31.50	33.00	30.00
B. Monthly mean surface salinities ($^0/oo$)								
Station I	14.24	23.50	26.17	28.05	32.54	33.33	34.31	31.00
Station II	5.61	10.22	14.60	20.70	26.63	29.31	29.34	27.00
Station III	**Fresh water**			5.01	11.31	12.63	8.19	*
C. Displacement volumes of zooplankton (ml/m^3)								
Station I	1.90	3.00	2.00	5.00	16.50	8.50	3.75	3.30
Station II	2.70	2.30	5.25	11.50	40.00	35.00	41.20	48.70
Station III	*	*	*	2.00	8.00	9.00	4.00	*
D. Abundance of zooplankton numbers/m^3								
Station I	433	4230	1221	242	9375	4110	1310	3140
Station II	185	1181	2973	14357	5966	15760	4965	7130
Station III	*	*		*	165	1200	900	400

* No sampling due to prevalence of freshwater conditions

could be found only from February to June. Maximum salinities were recorded during summer (April-June) (Table IB).

ZOOPLANKTON BIOMASS

Zooplankton biomass showed a conspicuous peak in November-December whereas phytoplankton was most abundant in March-April. Corresponding with the post-monsoon period organisms start to enter the estuary from September onwards. The early immigrants were mostly euryhaline crustaceans. Later, with increasing salinity typical littoral groups become established in the estuary. In March and April when stable hydrographical conditions prevailed, the zooplankton biomass and numerical abundance were markedly high. Comparing stations I and III, to station number II the latter had fairly stable conditions for most of the year and therefore maintenance of populations seems possible here (Table I C, D).

PLANKTON SPECIES

Hydromedusae, represented by *Phialidium hemisphaericum*, *Liriope tetraphylla*, and *Bougainvillia fulva* were present, almost constantly, during the period of study. Copepods were very abundant, dominant species were: *Eucalanus elongatus, Paracalanus parvus, Acrocalanus gracilis, Pseudodiaptomus binghami, Labidocera acuta, Pontella fera, Acartia clausi, A. erythrea,* *A. sewelli, Corycaeus speciosus, Macrosetella gracilis* and *Euterpina acutifrons*. Among the adult crustaceans mysids were seen in fairly high numbers in the samples collected at night. The common species encountered were *Rhopalophthalmus kempi, Mesopodopsis orientalis, Gastrosaccus muticus* and *Potamomysis assimilis*. Except for *Lucifer hanseni* which was present in large numbers for most of the year, all decapod crustaceans were in larval stage. *Sagitta enflata* and *Sagitta robusta* were common among chaetognaths. Non-crustacean invertebrate larvae, seen in the samples invluded members of Echinodermata, Mollusca, Brachiopoda and Polychaeta. Soon after the start of the monsoon due to large scale flooding of the rivers, the inshore waters of the Bay of Bengal register a marked drop in salinity to about $17^{0}/oo$ (Ganapati & Murthy, 1954). The migration of plankton populations is facilitated by the regular sequence of high tides which tends to carry these organisms from the nearshore area into the estuary. The extensive back waters near the mouth of the Godavari River affords good shelter for many organisms during the flood season and prevent them from being washed out of their normal habitat. Panikkar (1951) studied the physiological adaptation of estuarine organisms and made a note on the role of backwaters in maintaining stocks of planktonic forms, as a refuge during unfavourable conditions. From the studies made (Chandramohan, 1983) on the biology of the mysid *Rhopalophthalmus kempi*, it was obvious that the juveniles of this species enter the estuary during November from the backwaters, as this species is not normally found in the inshore area. The same is observed for *Potamomysis assimilis*. Surely estuaries are more productive than adjoining bodies of freshwater or sea (Abbott & Dawson, 1971). Since there is a net seaward movement of water, most of the plankton with nutrient rich waters from the estuaries are pushed into the neritic zone, during flood season. Only fifteen species out of sixty copepod species recorded in the present study were endemic to the estuary inhabiting euryhaline areas. We found freshwater species from the upper regions and also neritic species entering the estuarine environment. Occasional migrants from the neritic waters were also seen in the estuaries (Chandramohan, 1977).

The estuaries bordering the Bay of Bengal are peculiar in their ecological nature since they contain a rich variety of organisms and contribute to the enrichment of populations in the near shore area. They also transport large quantities of nutrients downstreams towards the sea, during monsoon periods.

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LATITUDINAL VARIATION IN DIVERSITY AND BIOMASS IN IKMT CATCHES FROM THE WESTERN INDIAN OCEAN

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INTRODUCTION

It is widely stated that in general there are more species of plants and animals at low latitudes than at high and that biomass and/or productivity are the inverse of diversity (Fischer, 1964; Pianka, 1966; Pielou, 1975;1979). The applicability of these hypotheses is examined with reference to data derived from catches, particularly of midwater fishes, taken by an IKMT during two North-South transects in the western Indian Ocean.

METHODS

Collections were made during cruises 3 and 6 (Fig. 1) of the R.V. ANTON BRUUN as part of the U.S. program in Biology of the International Indian Ocean Expedition in 1963 and 1964 (narrative and final cruise reports containing station data are presented in Anonymous 1964a, 1965a for cruise 3 and Anonymous 1964b, 1965b for cruise 6). Diversity is based on species richness, numbers of midwater fish species in each total catch and/or catch fraction; limitations of the data prevent consideration of species evenness. Samples were sorted in the laboratory and examined by specialists who distinguished species classified in more than 35 families (data in the author's files)

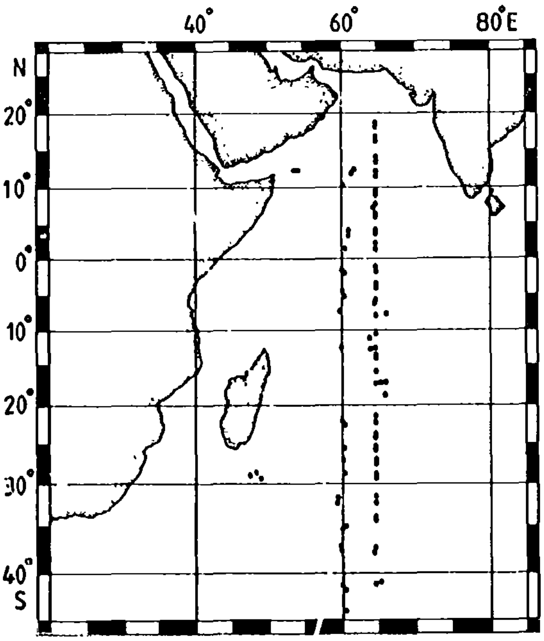

Fig. 1 IKMT stations occupied during cruises 3 and 6 as part of the U.S. Program in Biology of the International Indian Ocean Expedition.

Sources of error include variable lengths of tows, unequal absolute species pools, unequal population densities, variable availability to gear, patchiness, catch contamination, incomplete information on net time at various depths, variation in relative vessel speed during trawls, and incompletely known taxonomy.

RESULTS

In this connection data are presented on numbers of species caught, biomass, primary productivity, and hydroghaphy.

SPECIES DIVERSITY

Latitudinal variation in absolute number of species caught is illustrated in figure 2 A measure of diversity that takes into account fishing effort is number of species per hour, illustrated in figure 3.

Greatest diversity appears to occur between 7.5°N latitude and 12°S latitude for catches between the surface and 1000m and between the surface and depths between the surface and greater than 1000m, both dependent upon and independent of fishing effort. Catches independent of effort from the deep fraction of trawls fishing between the surface and depths greater than 1000m do not vary notably with latitude.

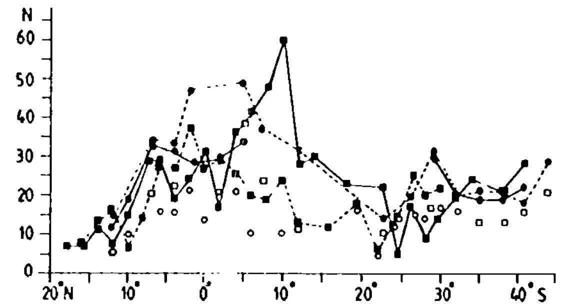

Fig. 2 Numbers of species of midwater fishes caught during two north-south transects in the western Indian Ocean. Solid dots and squares connected by solid lines are catches between the surface and 1000m during cruises 3 and 6, respectively. Solid dots and squares connected by dashed lines are catches between the surface and depths greater than 1000m during cruises 3 and 6, respectively. Open squares and circles are the deep fraction (a variety of depth intervals between 150-3500m) of trawls fishing between the surface and depths greater than 1000m during cruises 3 and 6, respectively.

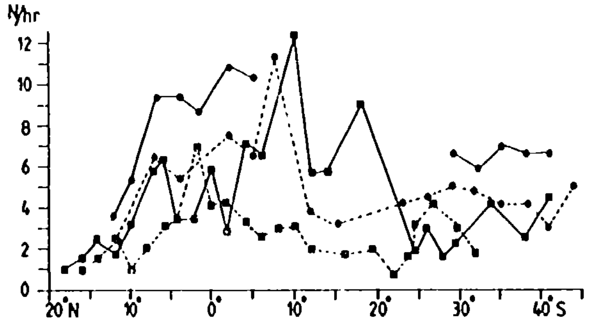

Fig. 3 Numbers of species of midwater fishes caught per hour of trawling during two north-south transects in the western Indian Ocean. Dots and squares connected by solid lines are catches between the surface and 1000m during cruises 3 and 6, respectively. Dots and squares connected by dashed lines are catches between the surface and depths greater than 1000m on cruises 3 and 6, respectively.

BIOMASS

Milliliters per hour caught of fishes and invertebrates combined is illustrated in figure 4.

For shallow tows a biomass peak occurs at 1.5° S latitude. Biomass tends to be low between 12° S latitude and and 23° S latitude.

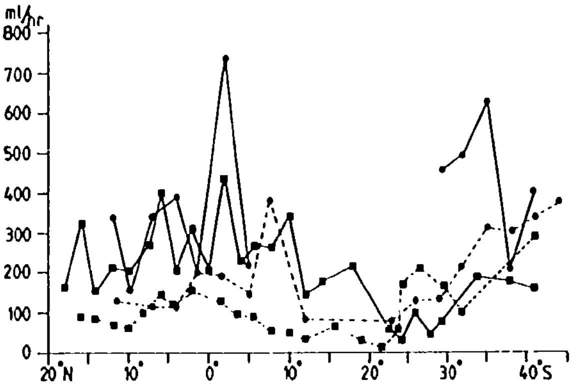

Fig. 4 Volumes of midwater fishes and invertebrates combined expressed as milliliters per hour of trawling during two north-south transects in the western Indian Ocean. Dots and squares connected by solid lines are catches between the surface and 1000m during cruises 3 and 6, respectively. Dots and squares connected by dashed lines are catches between the surface and depths greater than 1000m during cruises 3 and 6, respectively.

PRIMARY PRODUCTIVITY

Data on primary productivity during seven IIOE cruises (including 3 and 6) of the ANTON BRUUN in the western Indian Ocean have been presented by Ryther et al. (1966) from whom figure 5 of this paper is taken. Along the tracks of cruises 3 and 6, productivity is generally higher in the north, decreases to minimal amounts between about 15°S latitude and 27°S latitude, and then increases slightly.

HYDROGRAPHY

Several water masses were sampled at the various depths fished along the cruise tracks (Wyrtki, 1973). Surface water may be discounted, as epipelagic forms are excluded from this analysis and midwater fishes taken from

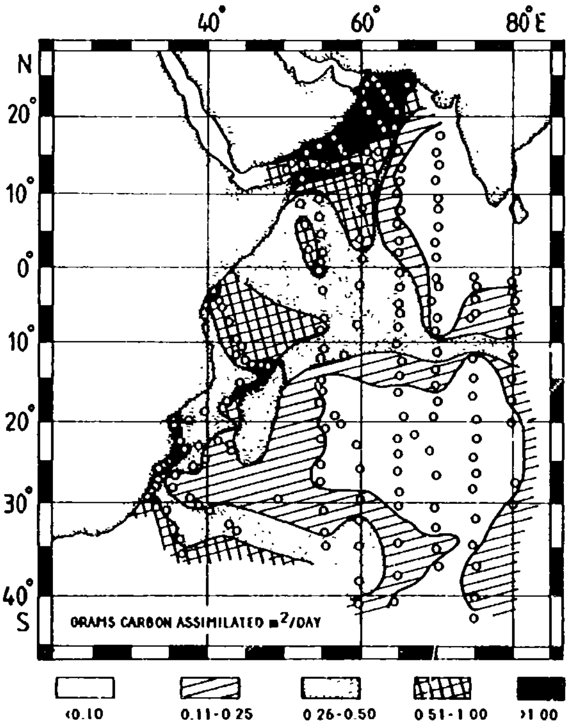

Fig. 5 Chart of the western Indian Ocean showing the positions of oceanographic stations occupied during Anton Bruun Cruises 2, 3, 4 A, 5, 6, 7, and 8 and the general level of primary organic production (Fig. 1 from Ryther et al., 1966).

surface layers during the night reside by day in deeper waters. From the northern ends of the transects to 8° - 10°S latitude shallow tows were mainly in North Indian High-Salinity Intermediate water of complex seasonal origin (Wyrtki, 1973). Deep tows throughout the transects fished partly in Deep water. South of about 10°S to about 40°S at the Subtropical Convergence shallow tows in the great subtropical anticyclonic gyre that has also been called the Indian Central water mass. At the far southern ends of the transects several stations were taken in the Subtropical Convergence.

DISCUSSION

Some possible causes, maintainers, and correlates of diversity (from an extensive sampling of the literature) are listed in Table I. It is unlikely that any are mutually exclusive. Correlates, positive or negative, are not necessarily causes but may contribute to maintenance. Knowledge about the biology of midwater fishes in general and limitations of the present data in particular preclude consideration of all the listed factors, but some can be addressed.

In general, mid-depths diversity and biomass are intermediate in the north with high productivity; a seasonally changing regime of monsoon winds (northeast in the winter; southwest in the summer) drives secondary variation in the pelagic environment; the deeper fauna, little influenced by the monsoons, lives in a more constant environment. Diversity at mid-depths is highest in equatorial waters, although somewhat offset to the south of the Equator, coinciding with the South Equatorial Current and the interface between Equatorial and Central water masses (hydrothermal front of Wyrtki, 1973), which is characterized in part by a shallow thermocline. In an interesting paper on seabird distribution in the Indian Ocean, Pocklington (1979) found highest bird diversity over the same area, with a similar pattern for certain copepods, euphausiids, and flying fishes, as well as highest albacore and yellowfin tuna abundance. He interprets his data in the light of environmental stability. But lowest diversity and biomass for midwater fishes occurred in low variability, high predictability Central water which has very low productivity and a deep thermocline. Diversity in very deep water did not vary notably with latitude; both in the north and south this fauna is in a stable and predictable environment; although early life history stages of some deepwater species pass time at shallower depths. Biomass, but not species diversity increases at the far southern ends of the transects, where the environment becomes less stable and the thermocline shoals.

With reference to table I, the environment is physically partitioned horizontally and vertically by density (defined with the temperature-salinity relationship) and vertically by temperature (as it relates to thermocline formation). The origins of these physical boundaries might have served as vicariant events and possibly date from the

Table I Some possible causes and correlates of species diversity taken from the literature. Various combinations are not included.

FACTOR	CAUSE	CORRELATE
Recruitment rate (speciation+immigration-extinction)	+	+
Number of niches	+	+
Niche size partitioning	+	+
Ecosystem complexity	+	+
Stability-predictability	+	+
Time	+	+
Area	+	+
Selection	+	+
Compation	+	+
Predation	+	+
Sympatric speciation	+	
Energy	+	?
Latitude		+
Temperature		+
Productivity		+
Population equilibrium		+

mid-Miocene (van Andel, 1976) in the present western Indian Ocean. Biological partitioning of the physically partitioned midwater environment is indicated by many and diverse species behaviors with some species resident above the thermocline, some resident in it or below it, some migrating to it or through it, some non-migratory, with variation in many individual species patterns related to size, sex, season and other variables. The vertical distribution of temperatures in the oceans was apparently important for speciation in past times (Lipps, 1970), as it is today (Angel, 1968). A growing literature on many aspects of midwater fish biology including space sharing (Badcock, 1970; Clarke, 1978; Karnella & Gibbs,1977; Legrand et al., 1972; Merrett & Roe, 1974 and Pearcy, 1964 are only a few examples) contains information that can be used to define niches, and several attempts have been made to do so formally. It seems likely that classical niche theory will go far towards explaining midwater fish diversity and distribution patterns making it unnecessary to invoke sympatric speciation or energy states (Wiley & Brooks, 1982) to explain the diversity of the midwater ichthyofauna.

The marine latitudinal diversity gradient as an expression of a species area curve has been proposed by Schopf et al. (1977); however well this explanation may serve for nearshore environments, it does not explain diversity in the midwater fish fauna, which occupies the most space of any in the world but is the least diverse (Cohen, 1970; Horn, 1972).

Productivity may be in some instances a significant correlate, but it is not on its own a cause.

An attractive explanation is that of Huston (1979). Within limits, competitive disequilibrium of populations (which may be driven by a variety of causes, in the present instance physical disturbances in the northern Indian Ocean) promotes disequilibrium of these populations, which inhibits compeltive exclusion and thereby maintains high diversity. The environment in the southern gyre is stable allowing a closer approach to population equilibrium, which allows competitive exclusion and lessens diversity. A situation that is quite to the contrary and not easily explained has been described for the highly diverse plankton community living in the central gyre of the North Pacific Ocean, an old and stable mass of water (McGowan & Walker, 1985 and papers cited therein). Diversity in plankton and in midwater fishes may be determined and maintained by different causes.

It is premature to speculate further on the signifiance of interactions of various of the tabulated factors. Multi-species-environment models constructed by fishery biologists are far from perfection, notwithstanding relatively few species and relatively large data bases. Comparable knowledge of the midwater fish community is in an even more primitive condition.

In summary, midwater fishes in the Indian Ocean do demonstrate higher diversity at low latitudes, but the overall pattern is modified by the physical and chemical regime. Isolation and niche diversification, suggested by Marshall (1963) are possible causes. Competitive dis-equilibrium of populations deserves further investigation. The latitude-diversity-biomass relationship is not clear.

ACKNOWLEDMENTS

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THE ROLE OF THE LEEUWIN CURRENT IN THE LIFE CYCLES OF SEVERAL MARINE CREATURES

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INTRODUCTION

Are the life histories of pelagic creatures adapted to ocean dynamics? To address this question the description of a current system having distinctive spatial and temporal characteristics was chosen to serve as a framework upon which to arrange the patterns of behaviour of several pelagic forms. Are there, for example, regions of correspondence in space and time to reveal that creatures match their activities to the properties of a current system?

THE LEEUWIN CURRENT

The Leeuwin Current (Fig. 1) has its source in the warm, low-salinity tropical waters off northwestern Australia and seasonally flows southward past western Australia and then eastward across the Great Australian Bight (Cresswell & Golding, 1980; Legeckis & Cresswell, 1981). The Current frequently interacts with offshore eddies and the resultant mixing produces a progressive decrease in its temperature and increase in its salinity along its path.

On its southward passage the Current is confined to the upper two hundred metres and flows above the continental slope with excursions onto the continental shelf. Its existence was first inferred by Saville-Kent (1897) from the tropical marine fauna and warm waters that he encountered at the Abrolhos Islands (28°30'-29°S). Other biological evidence for the Current was summarized by Maxwell and Cresswell (1981). It reaches the latitude of Perth, 32°S, in late April (autumn) and can be detected there by its warm, low-salinity waters generally until October (spring). As it approaches Cape Leeuwin it commonly accelerates to 1 $m.s^{-1}$ and then turns to the east with part of it spreading across the continental shelf. It has a distinct offshore front of several degrees Celsius and there its speed can exceed 1.5 $m.s^{-1}$. Farther eastward its passage across the Great Australian Bight is at a lower speed and not confined to the continental shelf. The overall progression of the Leeuwin Current waters is not rapid because of the formation of eddies and because of variations in flow rate. Satellite drifter data suggest that the fastest transits from North West Cape to Cape Leeuwin and then across the Bight are roughly 60 and 90 days respectively.

THE PELAGIC SPECIES

THUNNUS MACCOYII

Shingu (1967,1978) pointed out that the members of a species select their environment according to their size and maturity. Juvenile southern bluefin tuna prefer surface waters and, after spawning from September to March in the "Oka" fishing ground northwest of Australia, they move southward along the western coast of Australia to the Albany fishing ground. The distribution of larvae obtained on a recent survey of the "Oka" ground by the Fishing Agency of Japan is shown in figure 2. Comparing this distribution with figure 1 shows that the "Oka" ground lies within the source region for both the Leeuwin and South Equatorial Currents.

The Leeuwin Current could provide the reference frame and transport medium for the young fish as they migrate from the "Oka" spawning ground down to Albany. Inflow of the water and the juveniles into the Leeuwin Current could be expected to start in February. The arrival at Albany should be around May/June. Fish in their first and second years are caught off Albany in May/June with the smallest recorded

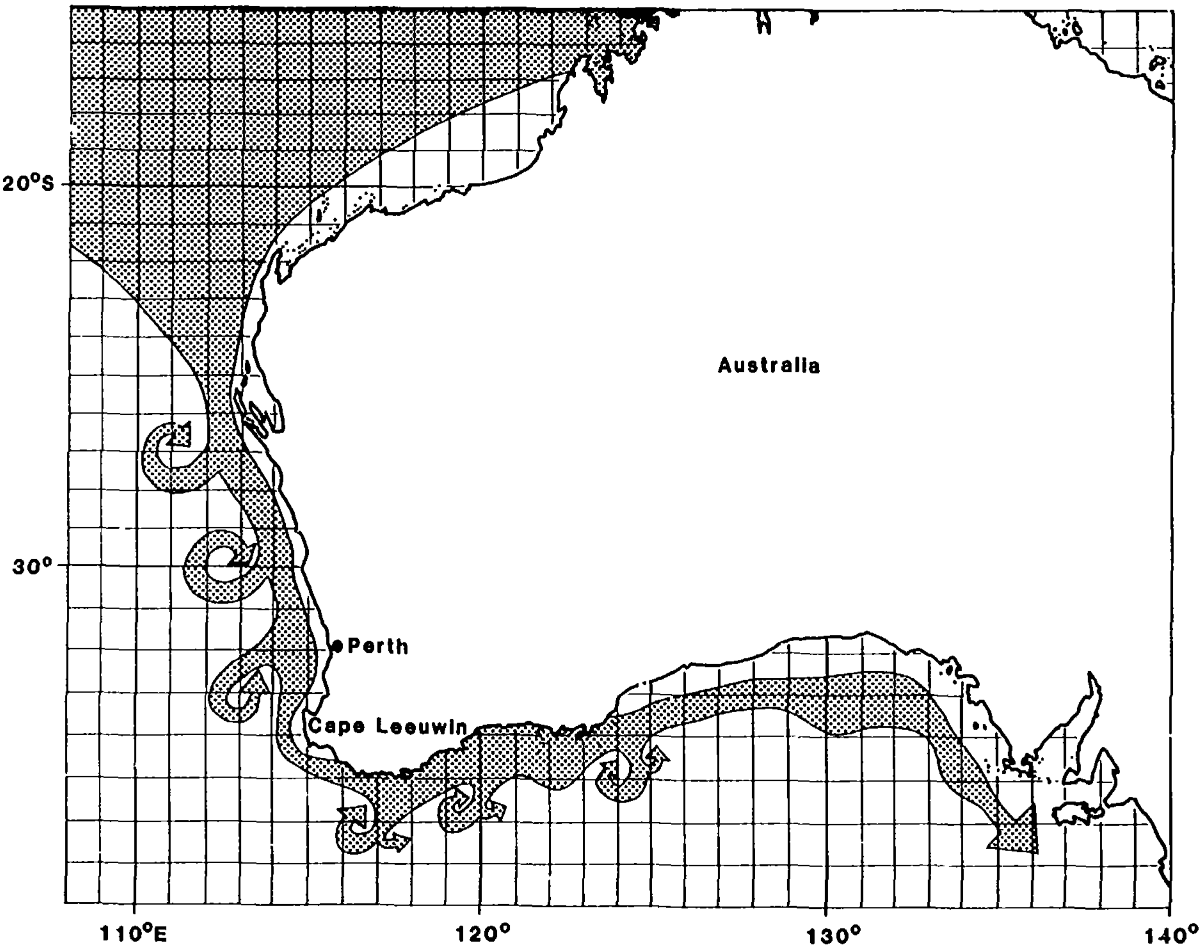

Fig. 1 A schematic picture of the Leeuwin Current drawn from information collected by research vessels, satellite tracked drifters, and satellite infrared sensors. The current has its source off northwestern Australia and consists of a shallow stream that is warmer and less saline than the surrounding waters. It mixes into eddies along its path and this leads to a progressive decrease in temperature and increase in salinity. The region off northwestern Australia also serves as a source for the South Equatorial Current.

fish (31.8 cm.) caught on March 25, 1951 (Serventy 1956), perhaps the result of an unusually early Leeuwin Current. The young fish may stay in the Albany region because of the availability of a food source which Serventy (1956) reported was mainly the pilchard (*Sardinops neopilchards*). The Leeuwin Current can serve to transport young tuna eastward on the next step of their migration: they are found off South Australia in their second and third years. Their decrease in numbers en route may be by losses into eddies offshore.

ARRIPIS TRUTTA

The western subspecies, *Arripis trutta esper* Whitley, ranges from southwestern Australia to southern Tasmania (Malcolm, 1960). In a pre-spawning phase the adults migrate westward (Fig. 3) travelling very close inshore. They are heavily fished by beach netting. Malcolm concluded that their spawning occurred in the Geographe Bay area in April and May because fully ripe fish were only found in that area and because the western migration appeared to terminate there. Munro (1963) found that the eggs hatched in a little

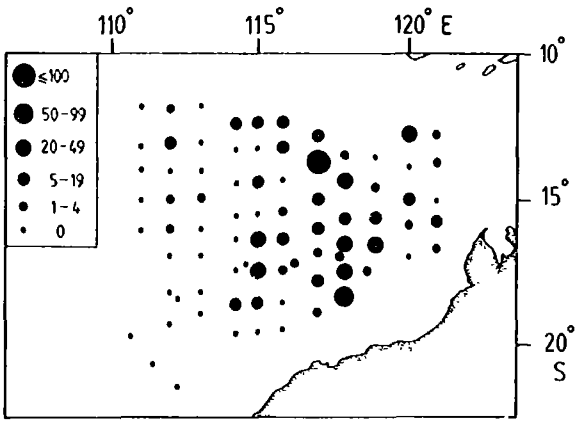

Fig. 2 The distribution of southern bluefin tuna larvae in the "Oka" fishing ground from October to December, 1983. The data combine both surface and subsurface tows of 20 minutes duration. (Reproduced from Fig. 12 of Fishing Agency of Japan, 1984.).

under 40 hours. The spawning, either fortuitously or by plan, is synchronized to the arrival of the Leeuwin Current and this would then take the larvae and juveniles eastward. The progression of the creatures to the eastern side of the Bight could take only 90 days if they remained in the waters of the Leeuwin Current. One year old fish are found as far east as Tasmania. The adult salmon return eastward after spawning (Fig. 4) and give rise to a second fishing season in the Albany region.

ARRIPIS GEORGIANUS

The time and location of spawning of this species is similar to that of the *Arripis trutta esper* Whitley. The spawning takes place north of Cape Leeuwin from February through June and so these larvae, too, will be carried off by the Leeuwin Current in the direction of South Australia where one and two year olds are found (Malcolm, 1973).

PANULIRUS LONGPIPUS CYGNUS

The eggs of this species hatch from November to March along the western coast of Australia between North West Cape and Cape Naturaliste (Phillips, 1981). The larvae rapidly disperse offshore, possibly due to wind-driven surface currents. Studies in 1976 showed that, although the larvae were widely distributed offshore, few, if any, larvae remained on or near the continental shelf from April to September. This period corresponds to the time when the Leeuwin Current flows southward intruding between the coast and the high salinity waters farther offshore. Rochford (1968) reported that larvae were salinity-dependent in their distribution: they were absent in waters of salinity less than 35.45 ‰S, such as found in the Leeuwin Current, and they were most abundant where the salinity was 35.80-35.85 ‰S. A year in which the Leeuwin Current continues to flow through into the normal settlement period could result in a failure of larvae to return to the coastal nursery areas.

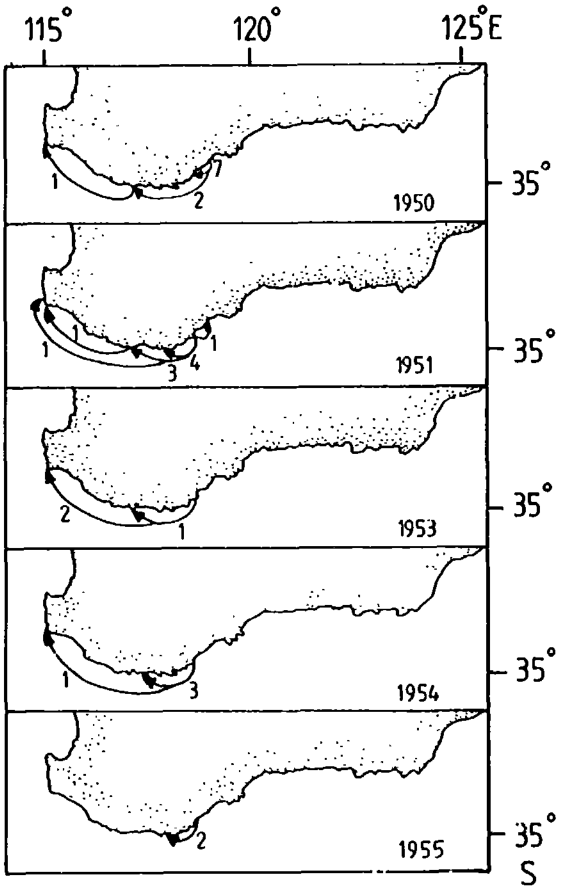

Fig. 3 The pre-spawning westward migration of salmon as indicated by tagging. Only movements of 25 miles or more are shown. The numbers denote the receptures at each locality. (Reproduced from Fig. 12 of Malcolm, 1960).

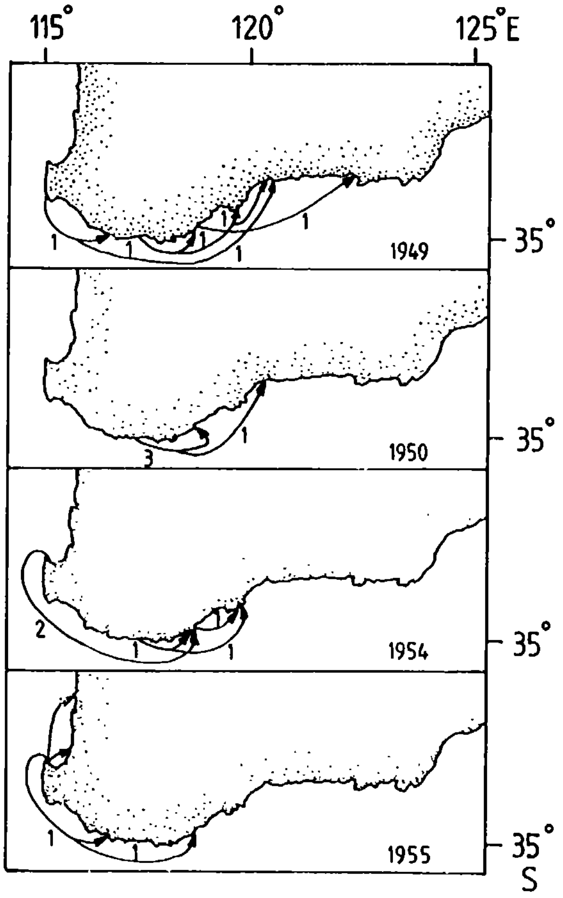

Fig. 4 The post-spawning eastward migration of salmon as indicated by tagging. The numbers denote recaptures at each locality. (Reproduced from Fig. 13 of Malcolm, 1960).

SUMMARY

The southern bluefin tuna (Thunnus maccoyii) may be adapted to spawn at a time that releases their young into the source waters of the Leeuwin and South Equatorial Currents. In the case of the Leeuwin Current the young fish are carried in its warm waters, down to the Albany fishing grounds where they reside up to one year before moving eastward, possibly also in the Leeuwin Current.

Spawning of the Australian salmon and herring (Arripis trutta and A.georgianus) may be adapted to place their young off southwestern Australia just prior to the arrival of the Leeuwin Current. The presence of one year old fish on the eastern side of the Great Australian Bight suggests that they are carried there by the Leeuwin Current.

The migration of the western rock lobster (Panuluris longpipes cygnus) is likely to be interrupted by the Leeuwin Current.

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LIFE CYCLE STRATEGIES OF OCEANIC DINOFLAGELLATES

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INTRODUCTION

Biologists have long recognized the importance of dinoflagellates as major primary producers in the oceans. Now there is increasing awareness that dinoflagellates are responsible for toxicity seriously threatening public health and commercial fisheries (e.g. Anderson, White & Baden, 1986).

Meanwhile, dinoflagellate studies have become established as an important research field in paleontology over the past 25 years. Fossil dinoflagellates have proved particularly useful in biostratigraphy and they are now one of the most important groups of microfossils used routinely in oil exploration. Both biological and paleontological interests in the group have concentrated on life histories since the realization, in the early 1960's, that it is the non-motile resting cysts in the life cycle (see Fig. 1) that fossilize (e.g. Dale, 1983).

Biogeography is an aspect of dinoflagellate studies of increasing interest for biologists and paleontologists. Biologists are concerned with factors regulating the distribution of toxic species, and reports suggesting that certain of these toxic phenomena may be spreading to hitherto unaffected areas of the world (Dale & Yentsch, 1978) have introduced an element of urgency in biogeographical studies. Paleontologists are interested in the biogeographical distribution of living dinoflagellate cysts as a model for interpreting paleobiogeography and paleoenvironments from the enormous amount of data accumulating from the fossil record.

Laboratory cultures are essential for detailed life history studies, but until recently only a few freshwater and neritic species had been cultured; information concerning oceanic species was restricted to traditional plankton studies. This paper results from new methods of culturing and observing oceanic dinoflagellates, for the first time allowing consideration of their life cycle strategies.

LIFE CYCLES IN FRESHWATER AND NERITIC DINOFLAGELLATES

Details on life histories of freshwater and neritic dinoflagellates have been summarized (Dale, 1983; Walker, 1985) and will not be repeated here. Although based on comparatively few observations these details suggest the generalized life cycle illustrated in figure 1, in which both asexual and sexual phases are recognized. It should be noted that this represents the free-living dinoflagellates; comparable information for benthic, symbiotic, and parasitic forms is scarce and outside the scope of this paper.

ASEXUAL LIFE CYCLE

Under optimal conditions dinoflagellates reproduce asexually by simple binary fission. Depending on the species and the environmental conditions, division may occur every 1-15 days. To withstand temporary adverse conditions (e.g. rapid shifts in temperature) cells may shed flagella and thecae to form non-motile cells referred to here as temporary cysts. Characteristically these form rapidly (within a few minutes to a few hours) and are of a more limited duration (probably days rather than months) compared with resting cysts produced in the sexual phase (taking days to form and able to survive for years).

SEXUAL LIFE HISTORY

For a long time sexual phases in dinoflagellates were not generally recognized, but it is becoming increasingly evident that sexual phases are probably much more widespread than previously

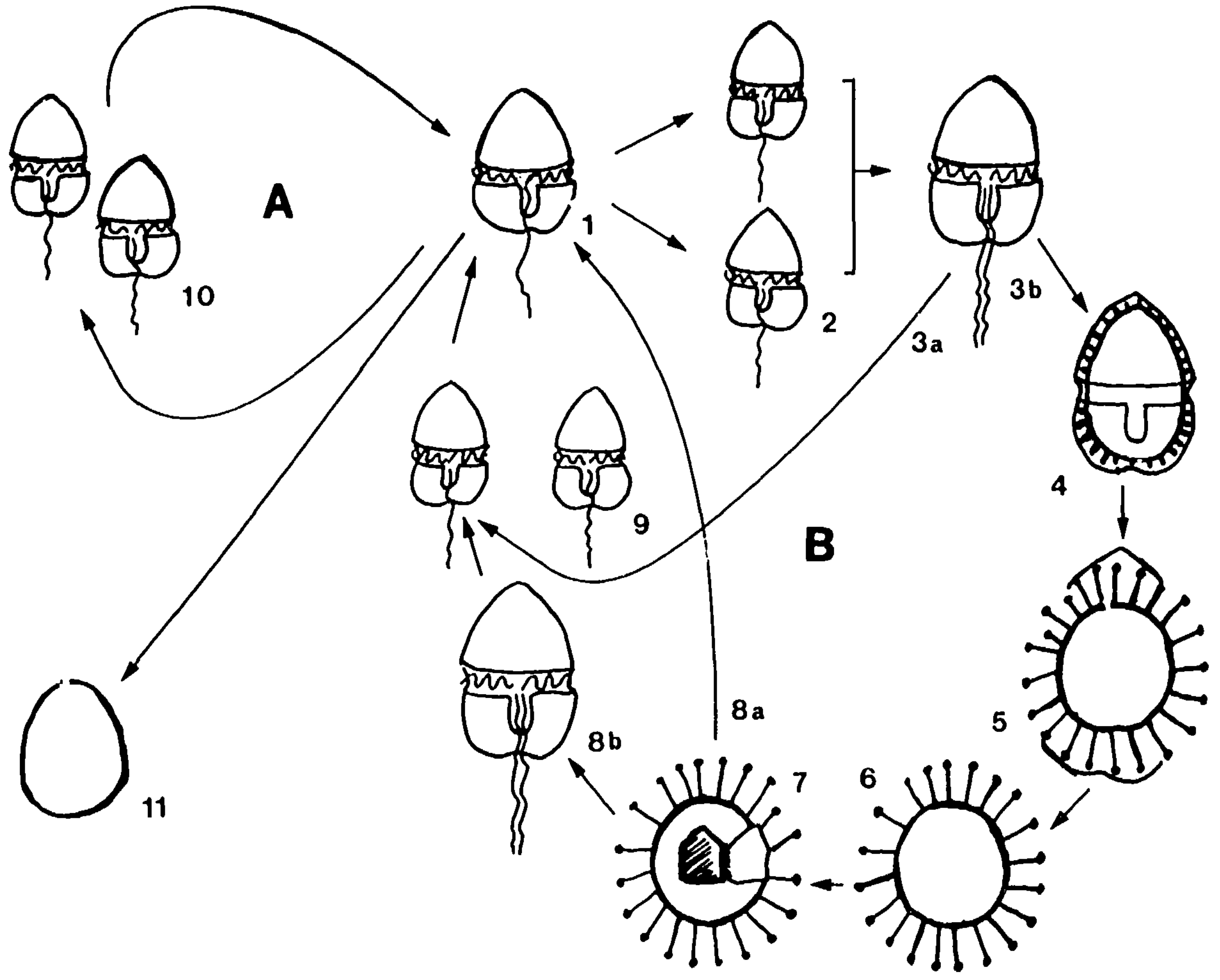

Fig. 1 Schematic diagram of basic dinoflagellate life cycles based on 20 freshwater and neritic species (modified from Dale, 1983; Walker, 1985). A= asexual phase with motile, planktonic vegetative cell (1) dividing by binary fission (10) and sometimes forming non-motile temporary cysts (11) to withstand environmental change. B= sexual phase with motile planktonic vegetative stage (1), producing gametes (2) pairs of which fuse to give planozygote (3). This eventually (3a) produces planktonic vegetative stage by reduction division (9) or loses motility and cyst formation begins (4) and may proceed (5) by expansion of cyst, producing resting cyst (hypnozygote) (6). Excystment (7) may produce a planozygote (8b), comparable with (3), which by reduction division (9) reestablishes planktonic vegetative stage (1), or in other species (8a) the reduction division is completed during encystment, allowing direct establishment of stage (1).

considered. That so far such phases have been documented from only 23 species is thought to reflect the difficulties of inducing the sexual life cycle in cultures and the painstaking demands of observing these in natural populations.

Known sexual cycles include gamete production, and ultimate fusion of pairs of these to produce a motile zygote (planozygote) (Fig. 1). The planozygote may develop in two different ways. In some species the planozygote undergoes meiosis producing the normal planktonic dinoflagellate (3a in Fig. 1). Although such planozygotes may characteristically have a somewhat larger size, double longitudinal flagella, darker colour, and large intercalary bands they often remain unnoticed in routine microscopic observations. In other species the planozygote loses motility and forms a resting cyst (hypnozygote), packed with food storage products such as starch and lipids, and often enclosed in a special resistant cell wall (3b-6 in Fig. 1). It is these resistant cyst walls that form the dinoflagellate fossil record. A few living cysts have been described with calcareous cyst walls (most likely calcite), and a group of fossil cysts with siliceous walls is known from Eocene sediments, but the majority of known living cysts have nonmineralized walls that may be strengthened by sporopollenin-like material (a unique class of biopolymers formed from carotenoids and/or carotenoid esters).

LIFE CYCLE STRATEGIES

"Life cycle strategy" is here used to denote the complex interreactions between life cycles and environments that allow the individual (and thereby the species) to survive. Within the basic life cycles summarized in figure 1, resting cysts offer at least three functions that are important for survival strategies: protection, propagation, and dispersion.

In temperate regions the "protective" role is illustrated by some species producing resting cysts that routinely overwinter at low temperatures which the motile cells cannot tolerate. The normal overwintering phase may last for up to 10 months (e.g. the warmer water element of summer plankton in Norwegian fjords), and cysts are able to survive at low temperatures for many years if not returned to conditions favourable for the motile stages. This also illustrates the "propagative" value of cysts acting as seeds; a resting period and dormancy ensures that a new plankton population can be established during favourable intervals in a fluctuating environment. In this way species may extend their ranges beyond the climatic boundaries in which motiles alone could survive year round.

Cysts generally function as benthic resting stages in freshwater and neritic waters, but as "fine silt particles" they presumably are sometimes transported by currents and "dispersed". They may thus help to extend a species range through invasion of new territory by dispersed cysts that later establish a motile population. Other stages in the life cycle also may be dispersed this way, but the greater resilience of cysts make them ideally suited to certain types of long transport and dispersal. Of particular concern to the problem of toxic species is the possibility that human agents may contribute to this type of dispersal, for example through ships (ballast, bilge water, on the hull, sediment on dredging gear) and through transplanted shellfish.

RECENT ADVANCES IN OCEANIC DINOFLAGELLATE STUDIES

Paleontologists are especially interested to see whether cysts, comparable to those routinely produced by freshwater and neritic dinoflagellates, are produced by oceanic forms, thereby suggesting the potential for an oceanic fossil record in deep sea sediments.

To many workers this seemed an unlikely possibility, but resting cysts clearly represent only one of two alternative strategies, and one that seems most suited to seasonally changing environments on a scale not considered typical for the pelagic realm. Furthermore, available evidence suggests that even within neritic dinoflagellates exposed to the large seasonal changes of temperate regions, less than 50% of the species produce resting cysts. Dale (1976) found 26 cyst types in bottom sediments from a Norwegian fjord where 57 species of motile dinoflagellates were recorded in long term plankton records. Most species are generally presumed to survive extensive periods of unfavourable conditions by a few vegetative cells providing a residual population (eg. temperate and boreal lakes in winter), and this would seem a more likely strategy for oceanic species. Walker (1985) suggested that oceanic species, in particular, may not have a sexual phase or may have an abbreviated sexual phase which lacks a hypnozygote (resting cyst).

Nevertheless, Wall et al. (1977) classified several cyst types as oceanic, based on their distribution in bottom sediments from a series of transects spanning coastal to deep sea environments. These cysts were found almost exclusively from the outer shelf to the deep sea, increasing as a proportion of the total assemblage seawards into abyssal depths.

The suggested presence of oceanic dinoflagellate resting cysts raised important questions biologically. These concern the function and strategy of cysts in the life cycles of oceanic dinoflagellates. Geologically, the main questions concern which types of cysts are produced, in what amounts, their degree of preservability, and their ultimate contribution to the sediment flux.

Traditional biological and geological studies were inadequate to investigate these questions. However, improved culturing methods have produced the first cultures of oceanic species (Tangen et al., 1982), and large sediment traps placed at different depths in the deep sea provided the first opportunity to sample living cysts and other stages sedimenting out through the deep sea water column (Dale, in the press).

OBSERVATIONS ON THE LIFE CYCLE OF *THORACOSPHAERA HEIMII*

One of the first oceanic forms to be studied in culture was *Thoracosphaera heimii* (Tangen et al., 1982). This species is commonly recorded from plankton in most oceans as distinctly small (10-25µm diameter), spherical, non-motile cells that are enclosed in a relatively massive calcareous wall. Most biologists have classified *Thoracosphaera* together with coccolithophorids, whereas micropaleontologists have variously regarded them as "non-coccolithophore nannoliths" (Haq, 1978) or dinoflagellate resting cysts (Fütterer, 1976). Tangen et al. (1982) showed that *Thoracosphaera* is a dinoflagellate with a life cycle unlike any other known for the group.

The life cycle is not yet completely known, but Tangen et al. (1982) showed that it includes a biflagellated motile phase identical with dinoflagellates, establishing the true identity of *Thoracosphaera* as a dinophyte. The role of this motile stage in the life history remains unknown, but of particular interest here is the asexual division phase illustrated in figure 2.

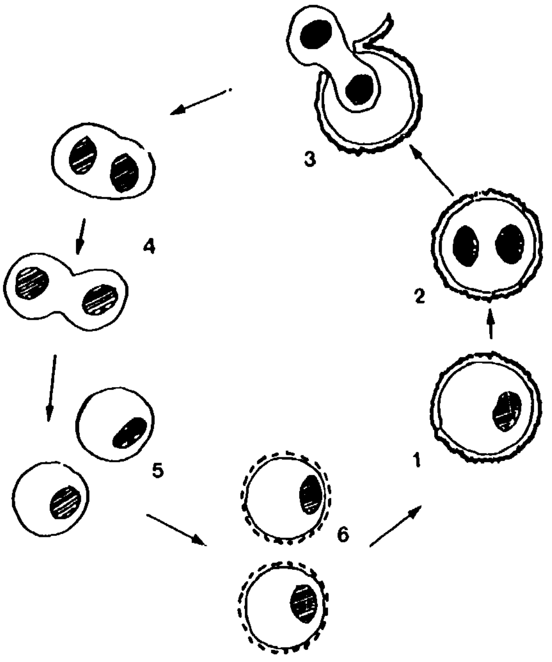

Fig. 2 Schematic diagram of part of the asexual phase in the life cycle of *Thoracosphaera heimii* (redrawn from Tangen et al., 1982). The uninuclear, non-motile vegetative stage, enclosed in calcareous shell (1) becomes binuclear (2), emerges from the calcisphere through opening (pylome) (3), divides (4) to give two cells (5) that quickly produces calcareous shells (6). The whole sequence was completed in about 10 mins in laboratory cultures.

Comparison of the asexual division phase in *Thoracosphaera* (Fig. 2) with its equivalent phase in other dinoflagellates (A in Fig. 1) shows binary fission as a basic similarity. The so far unique feature of *Thoracosphaera* is that the dominant planktonic stage (the vegetative stage) consists of a non-motile cell completely enclosed in a calcareous sphere (stage 1, Fig. 2). This contrasts sharply with the equivalent stage in almost all other dinoflagellates (i.e. a typical biflagellated motile stage enclosed by a cellulosic wall (stage 1, Fig. 1).

RESULTS FROM DEEP SEA SEDIMENT TRAPS

Samples, from large sediment traps placed at different depths in the deep sea, during the PARFLUX project, provided a unique opportunity to supplement previous nonquantitative information from the two extremes of near surface plankton tows and bottom sediments. For the first time, an attempt was made to document the remains of cysts and other life cycle stages of dinoflagellates sedimenting out through the deep sea water column and to compare them with cysts previously described from Recent deep-sea sediments (Dale, in the press).

Production of dinoflagellate resting cysts and thoracosphaerids (calcareous spheres referable to the genus *Thoracosphaera)* is of main interest here. Station data and sample data are shown in Table I. Three categories of remains of dinoflagellate life history stages: calcareous cysts, organic cysts (i.e. non mineralized resting cysts), and thoracosphaerids were counted (Table II).

Sediment trap samples yielded many cysts, supporting earlier observations by Wall et al. (1977) that cyst formation is not restricted to neritic dinoflagellates but includes oceanic types. The most striking feature of the recorded cysts was the overwhelming dominance of calcareous forms.

Calcareous cysts are unknown from freshwater, and in neritic environments they have attracted much less attention than the organic-walled cysts that are thought to dominate most regions studied. Prior to this work, evidence regarding the relative amounts of calcareous cysts versus organic-walled cysts was restricted to just a few studies from neritic environments. These suggested that calcareous cysts are relatively more important in tropical rather than temperate regions. Dale (1976) reported only one to two percent in a Norwegian fjord, whereas Wall & Dale (1968) found abundant calcareous cysts in tropical sediments, though never dominating the assemblage to the extent seen in the deep sea. At least six types of calcareous cysts were recorded from the sediment traps, but by far the most common type (accounting for over 90%) is only known from the deep sea. Abundances and distribution of these cysts strongly suggest they are regularly produced by oceanic dinoflagellates.

Very few organic-walled cysts were seen in sediment trap samples. Only one example was seen of the oceanic cysts cited by Wall et al. (1977). This was surprising since elsewhere they are commonly recorded from deep sea sediments and occasionally from slope water plankton. This may be explained if relatively few organic cysts are

Table I Summary of station data and samples used for deep sea dinoflagellate studies

STATION	PARFLUX $S_{1,2}$	PARFLUX E	PARFLUX P_1	PARFLUX PB
LOCATION	31°32.5'N	13°30.2'N	15°21.1'N	5°21'N
	55°55.4'W	54°00.1'W	151°28.5'W	81°53'W
OCEAN/BASIN	Sohm abyssal plain	Demerara abyssal plain	E.Hawaii abyssal plain	Panama basin
TERM	10/76-1/77	11/77-2/78	7/78-11/78	8/79-12/79
DURATION	75 days	110 days	98 days	112 days
TRAP DEPTH (m)	(372)	* 389	378	* 667
	* (976)	* 988	978	1,268
	*3,694	*3,755	*2,778	(2,265)
	5,206	*5,068	*4,280	*2,869
	*5,369		*5,582	*3,769
				*3,791
OCEAN DEPTH (m)	5,581	5,288	5,792	3,856
SEDIMENT	*Box core			

*Samples used for dinoflagellate studies. Trap samples represented size fraction <63μm (<250μm in S_{5369}).

Table II Dinoflagellate cyst and thoracosphaerid fluxes per m^2/day for trap samples documented in Table I.

Stat.	Trap-depth	Dinoflagellate cysts: organic	Dinoflagellate cysts: calcareous	Thoraco-sphaerids
S	1000m		6002	*
	4000m		8704	*
	5350m		2560	*
E	389m	14	5537	*
	988m	48	5809	*
	3755m	48	13169	*
	5068m	38	14546	*
P	3000m		1968	19391
	4500m		1567	14125
	5500m		401	2352
PB	667m	30	2392	30797
	1268m	152	2438	29399
	2869m	335	2591	33818
	3769m	290	3626	35824
	3791m	330	2337	24049

* not counted

produced, on a scale not covered by this type of sampling. Organic-walled cysts were seen in only two stations, represented almost entirely by unidentifiable spherical brown protoperdinioid cysts. *Protoperidinium* species are probably heterotrophic which correlates with the fact that the two stations mentioned are significantly nearer to continental land masses than are the other stations. These protoperidinioid cysts may be reflecting hitherto unrecognized concentrations of heterotrophs below the euphotic zone in such regions.

Most of the thoracosphaerids recorded (Table II) were small calcareous spheres of *T.heimii* or *T.granifera*. At stations P and PB (Table I) they were roughly ten times more abundant than dinoflagellate cysts. Though thoracosphaerids were not counted for stations S and E, many were observed incidentally and they are presumed to be similarly abundant at those stations. Distribution of thoracosphaerids in trap samples suggests a steady flux of these through the water column. Their much greater rate of production compared to dinoflagellate cysts is consistant with observations by Tangen et al. (1982) that they are vegetative stages (produced more often by asexual division) rather than resting cysts (produced less frequently by sexual division).

BIOMINERALIZATION AND SINKING STRATEGIES

Studies of sediment trap samples and *Thoracosphaera* in culture both suggest the somewhat surprising conclusion that routine production of non-motile stages is an important feature in the life cycles of several oceanic dinoflagellates. Observations from material in culture show the non-motile phases of *Thoracosphaera* to be normal vegetative cells. The cysts recorded from the deep sea sediment traps have never been studied in culture. However, they are morphologically similar to other dinoflagellate resting cysts. They are presumed to serve the same basic function of hypnozygotes in a sexual cycle, though obviously not as benthic resting stages at abyssal depths. Alternative suggestions for their mode of functioning are: 1) their buoyancy may allow them to remain suitably placed in the water column (significantly, only empty cysts were see sedimenting deeper in trap samples), or 2) they may complete their sexual function at a rate allowing excystment before the cyst sinks to a depth from which the emerging motile stage can no longer reestablish contact with shallower plankton (Dale, in the press).

Another surprising feature of oceanic life cycles was the heavy mineralization of non-motile stages. Biomineralization is known in only a few other dinoflagellates, mostly restricted to a few forms with siliceous internal skeletons, (e.g. Tappan, 1980: 250-256) and some other calcareous cysts (e.g. Wall & Dale, 1968). Thick calcareous walls suggest a possibility for a sinking strategy, least expected in oceanic dinoflagellates. Nevertheless, particularly since heavily mineralized non-motile stages figure in two different life history stages (vegetative and sexual) of two different groups of dinoflagellates, this may well represent a common sinking strategy coupled to biomineralization. Such strategies are found in other planktonic groups.

The major phytoplankton groups, diatoms, dinoflagellates, and coccolithophorids are geologically old, extending back through the Mesozoic Era. They have maintained their separate identities while presumably sharing the same environments because of basic, strong, equally viable differences within their total biologies; almost certainly including factors such as biomineralization and life cycle strategies. Considered from this point of view the groups may be characterized thus: diatoms utilize biomineralization as the basis for a non-motile sinking strategy, dinoflagellates generally do not utilize biomineralization but employ flagella in a swimming strategy, and coccolithophorids possibly utilize a combination of the two with both mineralization and motility combined, though the sinking strategy may predominate.

Smetacek (1985) summarized those features of diatoms that may be interpreted as constituting the basis for a sinking strategy, thus offering comparisons with the oceanic dinoflagellates. Of particular interest is the obvious value of the heavily mineralized frustule as balast for helping the diatom to sink. The heavily mineralized shells of thoracosphaerids and calcareous dinoflagellate cysts are here considered probably to serve a similar function, though the extent to which these cells can regulate their own buoyancy as do diatoms remains unknown. If massive biomineralization in thoracosphaerids and calcareous cysts does represent a parallel sinking strategy to that of the diatoms, other dinoflagellates with a combination of mineralized skeletons and flagella may be similarly paralleling the combined sinking/swimming strategies of e.g. coccolithophorids.

Smetacek (1985) also suggested other sinking mechanisms for diatoms that may have analogies with some other types of cysts known from neritic dinoflagellates. He noted "increased mucous secretion in conjunction with the cell protuberances characteristic of bloom diatoms leads to entanglement and aggregate formation during sinking; the "sticky" aggregates scavenge minerals and other particles during decent which further accelerates the sinking rate". Many cysts posses a variety of spines that certainly lead to entanglement (both with other cysts and debris) and aggregates, while several cysts are known that are coated with a mucous layer which scavenges minerals and other particles (e.g. Dale, 1977). Such mechanisms may also serve to help benthic resting cysts in maintaining their position in bottom sediments during the resting period, resisting possible washing out by bottom currents.

The advantages of the sinking strategy for oceanic dinoflagellates are not known but presumably they are similar to those forming the basis for diatom strategies. These may include removing the cell from nutrient poor waters of the euphotic zone at times of particular depletion to nutritionally richer waters usually found a little deeper in the water column, and advantages of long distance lateral transport (assuming a degree of buoyancy) to other regions of improved nutrients (e.g. upwelling).

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THE AZORES FRONT: A ZOOGEOGRAPHIC BOUNDARY ?

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INTRODUCTION

The zoogeography of the mesopelagic fauna of the N.E.Atlantic is reasonably well understood only for a handful of taxonomic groups (Ostracods: Angel & Fasham, 1975; Fasham & Angel, 1975; Fish: Backus et al., 1977; Decapod crustaceans: Foxton 1972; Casanova, 1977; Fasham & Foxton, 1979). Fasham & Foxton (1979) showed that the zonation of decapods sampled at 10° intervals from 10°N to 60°N along the 20°W meridian, could largely be explained in terms of the ocean's hydrography. Their >1000km spacing yielded faunal regions with apparently clear bounderies between them but on this scale the precise nature of the transition areas could not be determined. In this paper the boundary between two water masses is examined in greater detail with respect to the decapod crustacean faunal assemblages.

The area under consideration here is a region to the S.W. of the Azores on the eastern flanks of the Mid Atlantic Ridge (Fig. 1). Through this area runs an extension of the southerly return branch of the Gulf Stream and this gives rise to a permanent oceanic frontal region, referred to as the Azores Front (Gould, 1985).

PHYSICAL BACKGROUND

During 1980/81 the Institute of Oceanographic Sciences mounted a programme to investigate the Azores Front. It was found to be a meandering feature 20-50km wide, characterized by rapidly changing isotherm depths across it and high near surface currents of ≤40cm s^{-1} along it. On one side of the front lay Eastern Atlantic Water (EAW) typified by the 16°C isotherm depth of < 150m, on the other side lay Western Atlantic Water (WAW) with the 16°C isotherm >300m. Fasham et al. (1985) reported that the WAW was generally poorer in nutrients and had only 50-60% of the chlorophyll levels of the EAW. However, despite the potential for greater mixing in the front there was no evidence of consistently higher phytoplankton productivity levels in the frontal region. During May and June 1981 the front propagated westwards by some 55km, at the same time a 100km diameter EAW eddy was pinched off from a meander and moved westward at 2.2km d^{-1}.

NET SAMPLING

Five stations were occupied: in the WAW, in a WAW meander, in the front, in the EAW and in the newly formed EAW eddy. At each station a day and a night series of hour long net hauls were fished over 100m depth horizons to at least 1200m depth using an opening/closing multiple RMT 1+8 system (Roe & Shale, 1979).

RESULTS

A total of 56 species of decapods were identified from 126 hauls. Of these 34 spp. were cosmopolitan, seven occurred only at one station and, of the remainder, only two or three species showed any semblance of an EAW-WAW cline in terms of presence/absence. The abundance of the 15 dominant species from each station are given in Table I. Clearly the majority of abundant species were most numerous in the Front and scarcest in the WAW. This pattern is repeated in biomass as indicated by the displacement volume of animals contained under $10m^2$ of ocean surface from 0-1200m depth range averaged over day and night: WAW ($4.2cm^3$), EAW ($6.5cm^3$), W.Meander ($7.7cm^3$), E.Eddy ($8.3cm^3$) and Front ($9.4cm^3$).

Kendalls Rank Correlation was used to derive dendrograms of similarity between stations using

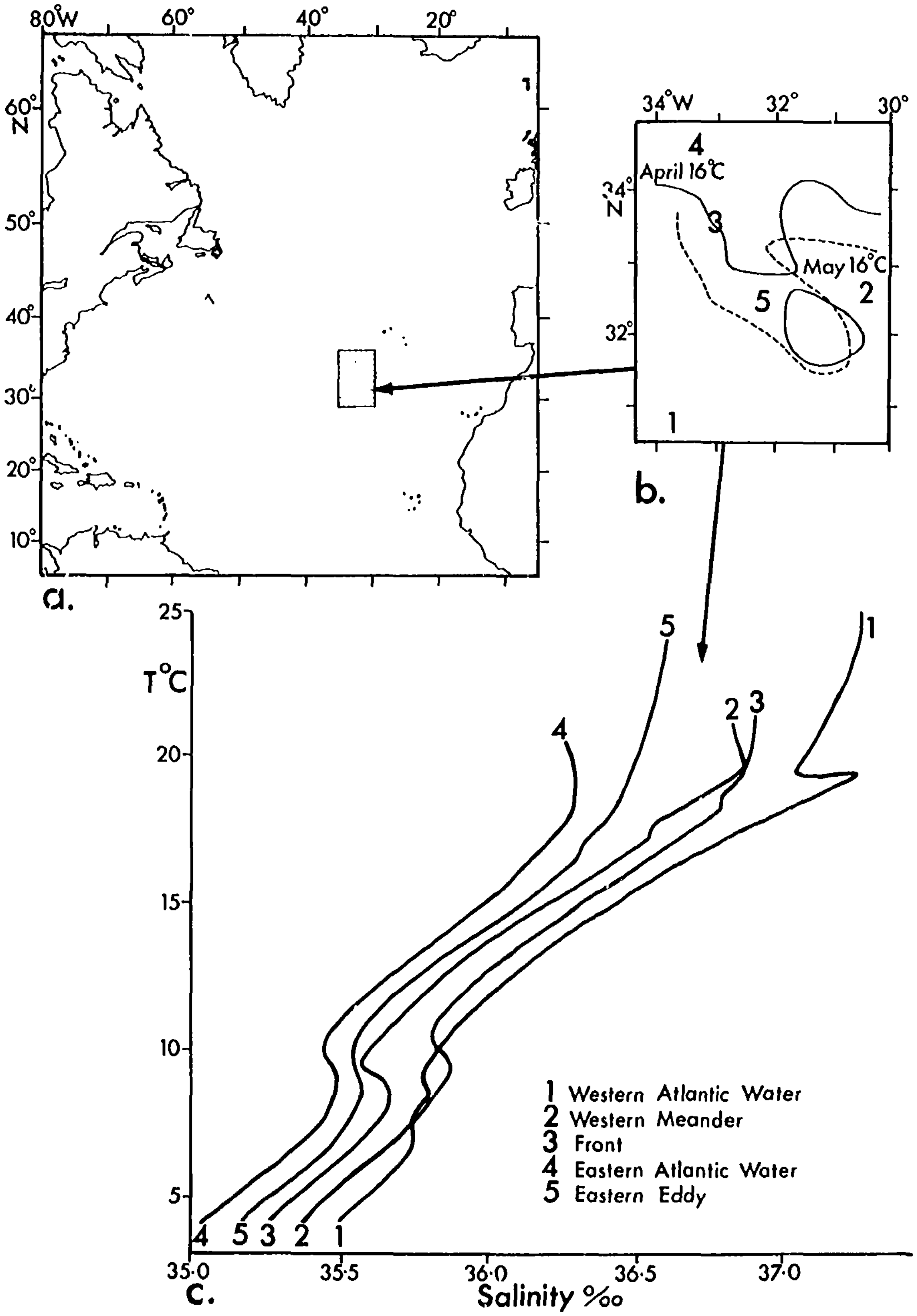


Fig. 1 a. The study area to the S.W. of the Azores. b. The position of the front during late Spring 1981 as defined by the location of 16°C isotherm at 200m. c. T/S curves for the five stations, a displacement of 0.1 0/00 is used to separate them. For station details refer to the Appendix.

Table I is compiled using the 15 most abundant species from each station. Values given are numbers of animals under $10m^2$ of sea surface. Bathypelagic species whose population ranges have not been fully sampled are denoted by an asterisk.

Species	**WAW** **10380**	**W.Meander** **10378**	**Front** **10376**	**EAW** **10379**	**E.Eddy** **10382**
Caridea:					
Acanthephyra purpurea	1.37	5.68	4.77	3.17	5.21
Acanthephyra pelagica	0.	0.19	0.61	0.69	0.03*
Acanthephyra stylorostratis	0.65*	0.15*	0.56	0.26*	0.12*
Systellaspis debilis	1.23	1.63	1.27	1.09	1.46
Oplophorus spinosus	0.36	0.51	0.65	0.66	0.70
Parapandalus richardi	0.48	0.71	0.54	1.0	0.45
Parapasiphaea sulcatifrons	0.14	0.35	0.77	0.67	0.42
Hymenodora gracilis	1.12*	0.71*	3.19*	4.69*	0.40*
Hymenodora glacialis	0.28*	*	*	0.08*	*
Sergestidae:					
Sergestes (Sergia)robustus	0.	0.06	1.77	0.05	0.24
Sergestes splendens	0.45	1.07	0.68	1.04	1.20
Sergestes japonicus	0.25	1.70	6.50	1.79	1.11
Sergestes tenuiremis	0.13	0.52	0.28	0.16	0.72
Sergestes (Sergestes)vigilax	0.30	0.33	0.98	1.57	1.01
Sergestes sargassi	0.12	1.27	1.89	1.35	0.62
Sergestes henseni	0.12	0.17	0.56	0.05	0.06
Sergestes curvatus	0.13	0.61	0.25	0.79	0.55
Sergestes atlanticus	0.06	0.12	1.95	1.31	0.83
Petalidium obesum	0.42*	0.10*	0.37*	0.16*	0.13*
Penaeidae:					
Bennadas elegans	0.01	0.23	3.76	1.91	0.96
B. valens	0.39	4.51	2.58	1.95	2.26
Bentheogennema intermedia	0.99	6.58*	3.18	5.18	4.05*
Funchalia villosa	0.32	0.24	0.05	0.26	0.18
Luciferidae:					
Lucifer **sp.(larval stages)**	2.90	0.25	0.08	0.28	0.14

the standardised totals of the 20 most abundant species (Fig. 2). For both adult and non-adult animals the WAW stands apart from the others and the EAW and E.Eddy are linked together in both cases. Although greatest overall similarity occurs between Frontal and W.Meander adult faunas this relationship is of less significance for non-adult stages.

Figure 3 shows the distributions of a selection of species typifying the main patterns of abundance across the front. Among the three major decapod taxa the robust diel migratory carids exhibited the least diminution toward the WAW. *Acanthephyra purpurea, Oplophoreus spinosus, Parapandalus richardi* and *Systellaspis debilis*, whose vertical ranges are largely confined to the top 1000m of the water column,all deepen slightly toward WAW in a trend common to the >9°C isotherms, this is most pronounced in the nighttime distributions which are shallower. Certain bathypelagic carids also change across the front, *A. pelagica*, which at these latitudes displays only slight diel migration, shoals and becomes more numerous toward the EAW. Conversely, the non-migratory *A. stylorostratis* shoals and becomes numerous in the WAW, these latter two species appear to be mutually exclusive. All three *Acanthephyra* species are abundant in the front although they are segregated by depth.

Unlike the study by Griffiths and Brandt (1983) in the East Australian Current, an analysis of length/frequency of carapace length for the most common carids revealed no significant differences in size structure between the five stations. Likewise the size and ratios of gravid to non-gravid females indicate that the same populations were sampled at each of the five stations.

Gennadas elegans a deep mesopelagic species and exhibiting no diel migratory habit at these latitudes was the most drastically affected of the *Gennadas* group by the transition from EAW to WAW. Poorly represented in the W.Meander, it was virtually absent in the WAW proper. *G. valens*, however, displayed extensive vertical migrations, was scarce in the WAW, but very abundant in the W.Meander. The bathypelagic species *Bentheogennema intermedia* was also scarcest in the WAW but most abundant in the W.Meander.

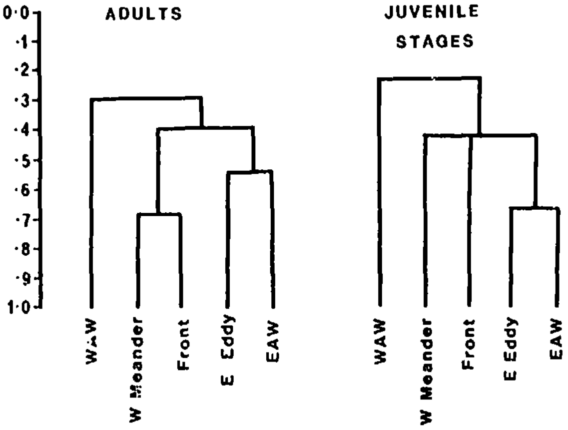


Fig. 2 Similarity relationships between the faunas of the five stations derived from Kendalls Rank correlation.

Apart from several of the larger *Sergia* spp. the sergestids also were scarce in WAW. Two species, *Sergia robustus* and *S. japonicus*, a migrator and non-migrator respectively were markedly more abundant in the Front than elsewhere.

DISCUSSION

During the past two decades it has become increasingly clear that the traditional view of stable and homogeneous oceans can be quite erroneous. Mesoscale features on a scale of 10s to 100s of km and months to years in duration have been reported in all the oceans, and the N.E. Atlantic is no exception (e.g. Madelain & Kerut, 1978; Gould, 1985). Horizontally, faunal transitions may be broad averaging out the effects of any mesoscale activity or narrow but exhibit variability on similar scale to the hydrography. In studies of both the Gulf Stream Rings (e.g. Wiebe et al., 1976) and the East Australia Current (e.g. Griffiths & Brandt, 1983) biological variability has been observed on a similar scale to that of the hydrography. Mesoscale variability has also been strongly suspected when there have been unexpected faunal discontinuities during otherwise routine sampling (Angel, 1977). The decapod assemblages considered here provide evidence for both slow and rapid response to such mesoscale activity.

Depth(s) of habitation and vertical mobility may, to an extent, determine geographical distribution as differences in the current shear with depth can affect patterns of dispersal (Miller, 1970). The vertically migrating carids are physiologically adapted to cope with a wide T/S range so, to these animals, the front represents no major obstacle. Faunal change for them, if any, across the front is only gradual. Vertical migration, however, is modified as there is a slight downward trend in the upper depth limit following the pattern in isotherms; this has been noted elsewhere (e.g. *Acanthephyra* spp. Foxton, 1972 and more generally; chaetognaths,

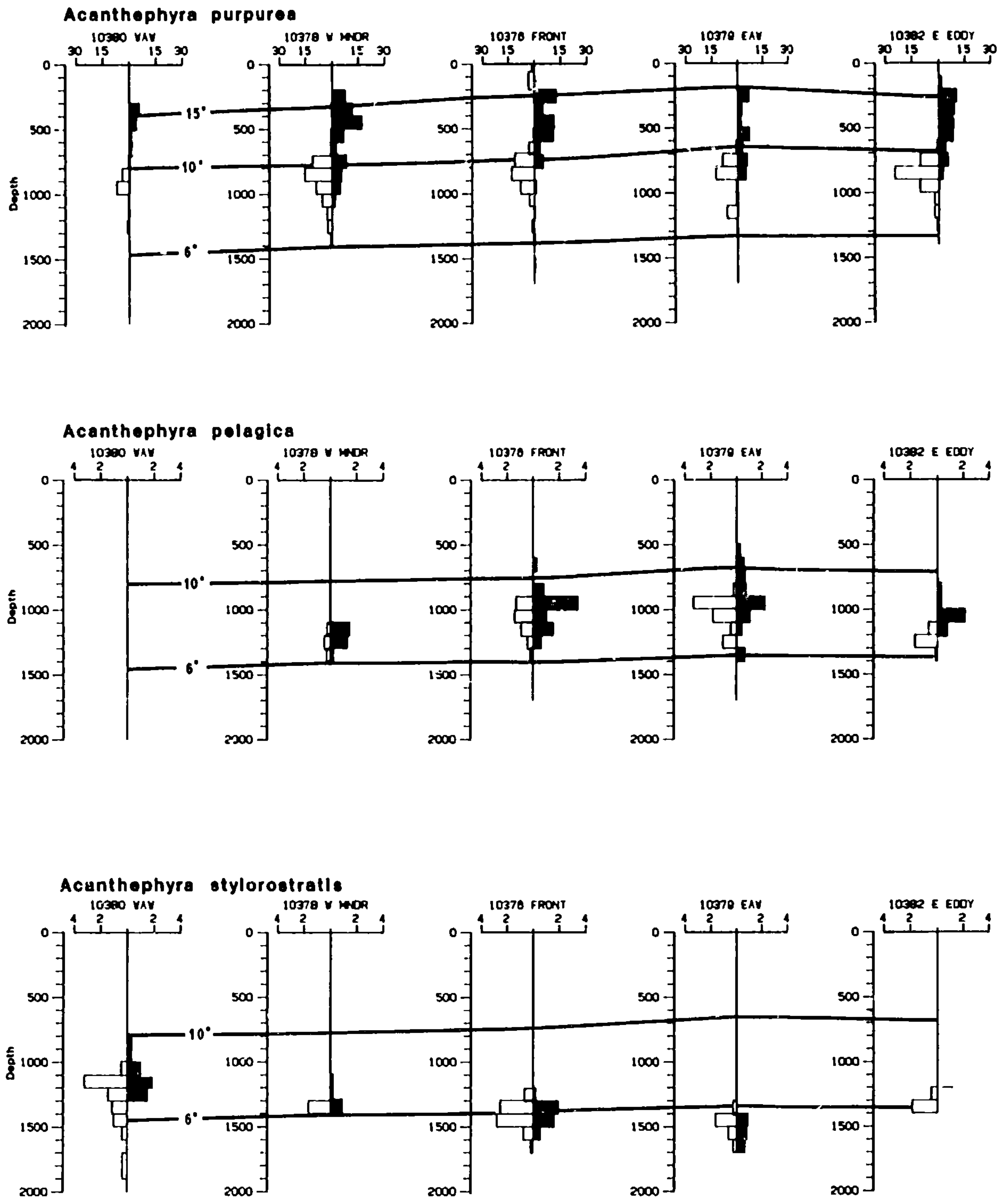
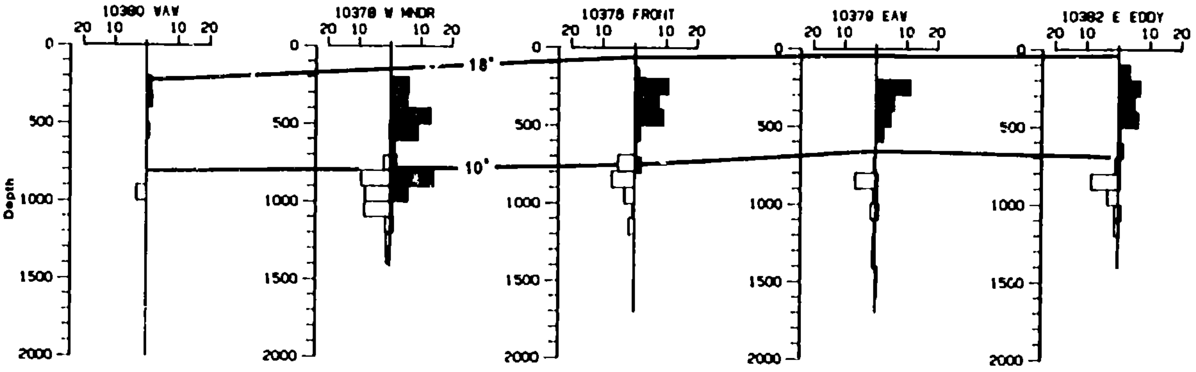
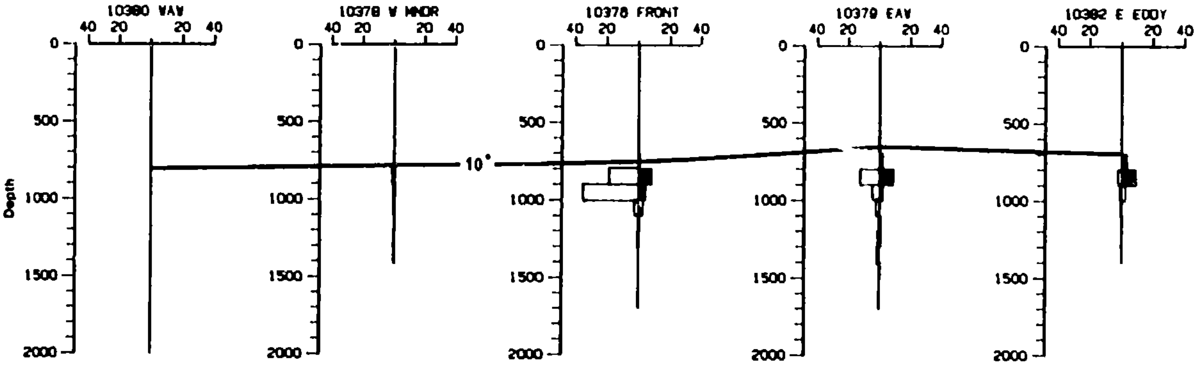


Fig. 3 Distribution of selected species across the front. Histogram bars are nos. $10^4 m^3$ of water filtered. Depth is in meters. Unshaded histograms: Day, shaded histograms: Night.

Gennadas valens



Gennadas elegans



Bentheogennema intermedia

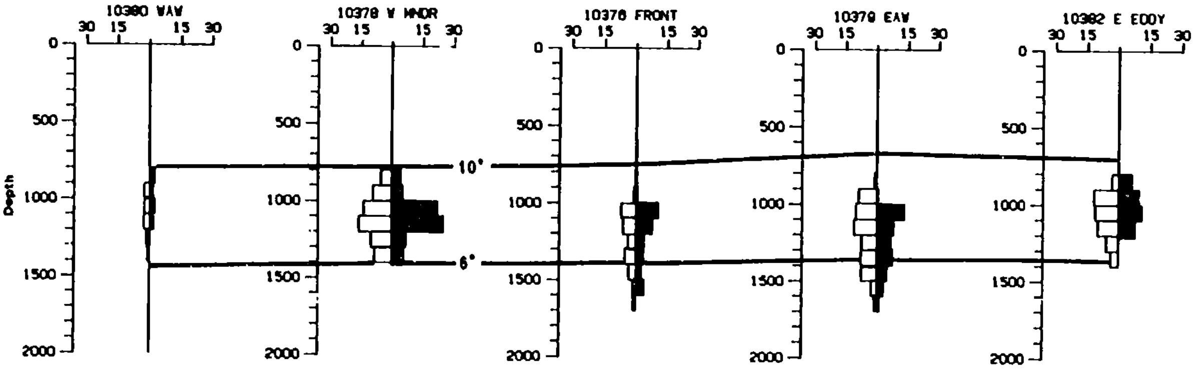
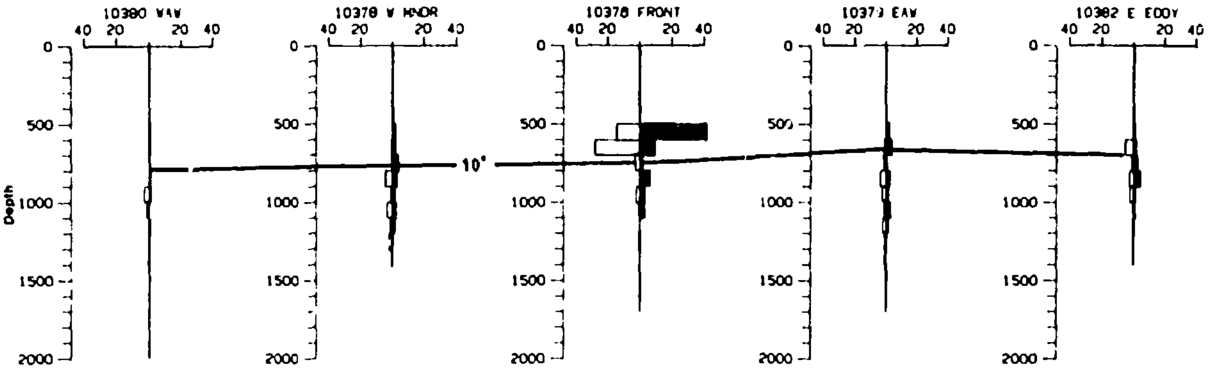
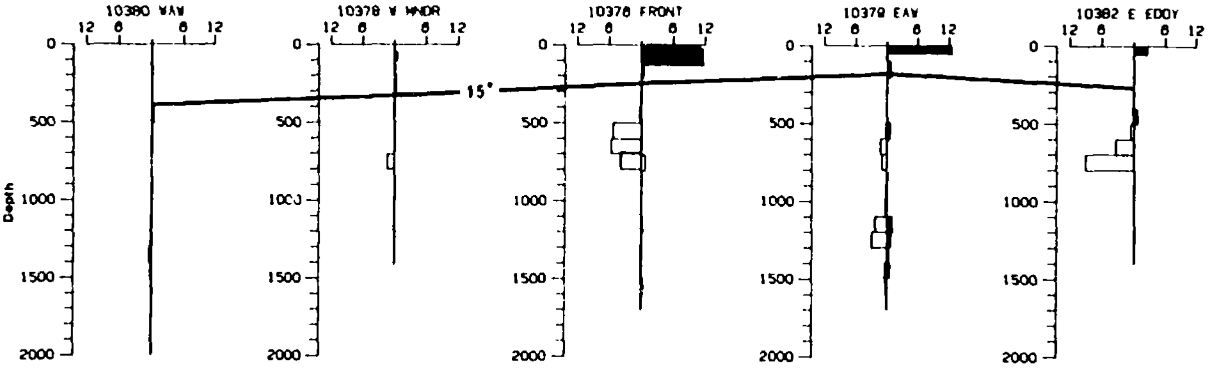


Fig. 3 continued

Sergia japonicus



Sergestes atlanticus



Sergestes vigilax

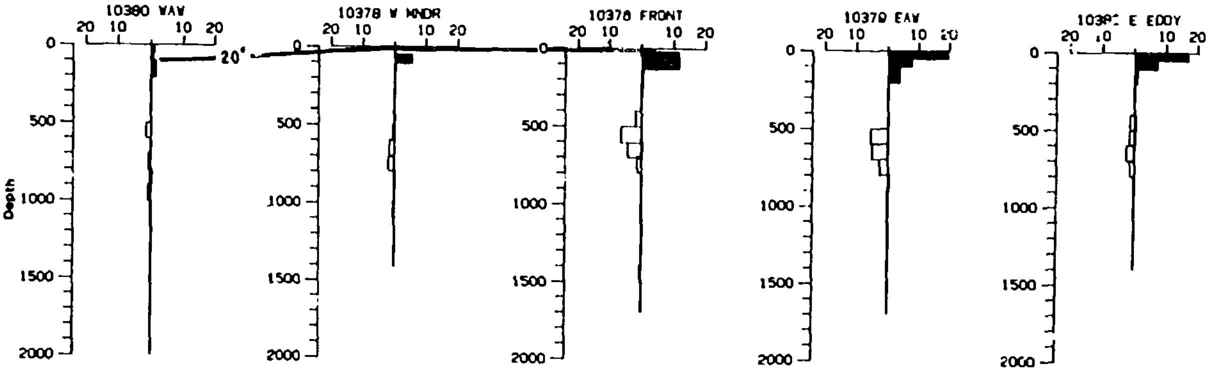
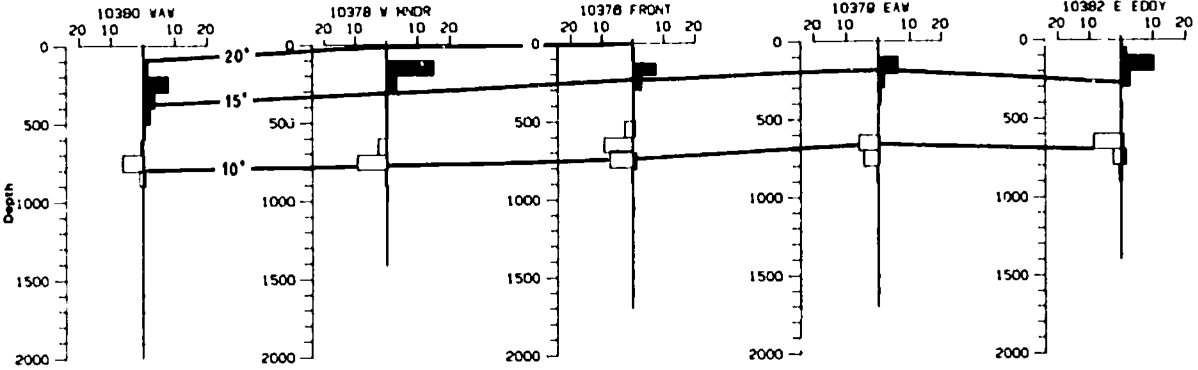
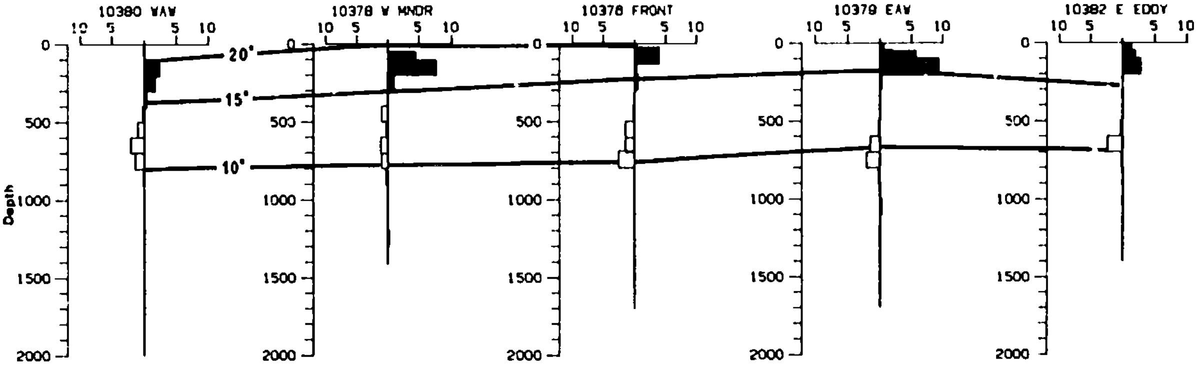


Fig. 3 continued

Systellaspis debilis



Parapandalus richardi



Sergia grandis

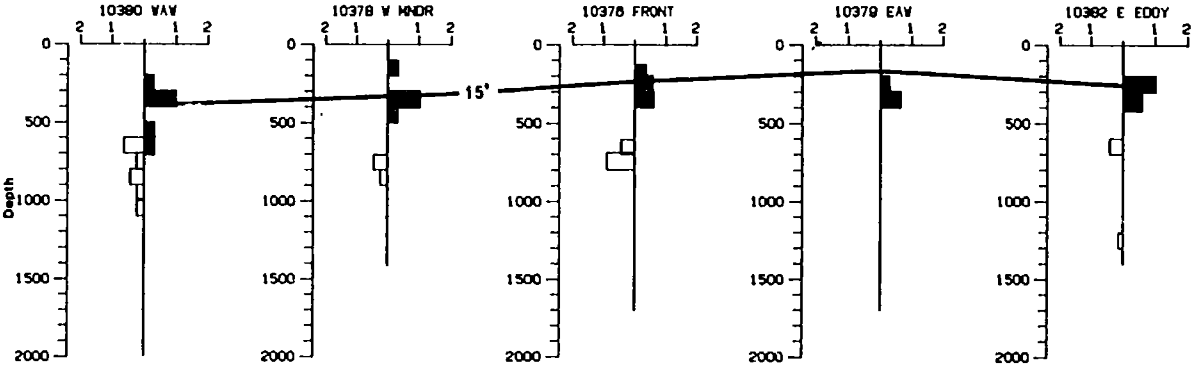


Fig. 3 continued

Pierrot-Bults, 1975; euphausiids, Wiebe & Flierl, 1983). As non-selective carnivores, (other than for size of prey; Foxton & Roe, 1974; Roe, 1985) the vertically migrating carids may be particularly trophically adaptable across the front.

There are examples in which the migratory and non-migratory habits are exhibited by species which are congeneric and it is the deeper, non-migratory species that are most restricted in distribution across the front. *Acanthephyra pelagica* only a partial migrator and *A. stylorostratis* a non-migrator, are more abundant in the EAW and WAW respectively, both reside mainly below 800m. *A. purpurea,* however, which undergoes extensive vertical migrations is more evenly distributed between the five stations; note that in the front all three species thrive but are vertically segregated. Amongst the *Gennadas* type species, *G. valens* occurs in all five stations (although scarce in WAW) and performs vertical migrations similar to those of *A. purpurea*. *G. elegans,* however, which dwells below 800m and does not migrate in this area, is scarce in the W.Meander and absent from WAW. It is noticeable that faunal differences across the front are most evident below 800m despite only very small differences in T/S relationships at this depth.

One could speculate that the scarcity of *Gennadas* in the WAW may be in part due to their high degree of detritivory (Foxton & Roe, 1974; Heffernan & Hopkins, 1981; Roe, 1985). Detritus, high in faecal material may be particularly lacking in WAW because of the generally lower productivity of these waters. The scarcity of sergestids, particularly small *Sergestes* spp. in WAW and W. Meander is not easily accounted for. Most species are diel vertical migrators and thus able to cope with a considerable T/S range. Gut analyses are few but indicate a diet of small micronekton and plankton with a degree of detritivory (Roe, 1985).

The greater abundance in the front and the two other stations between EAW and WAW is difficult to account for on available evidence alone. Griffiths & Brandt (1983) reported greater numbers of some decapod species and higher C:N ratios in the edge region of an eddy, caused possibly by the enhanced primary productivity in the edge region (Tranter et al., 1983). This higher productivity, they argued, could be transmitted through to higher trophic levels (Boyd et al., 1978). In this study no such enrichment was found in the region of the front (Fasham et al., 1985), however, it is unlikely that the increased micronekton resulted from a past phytoplankton enrichment in the immediate vicinity as advection in the relatively swift frontal currents would tend to be dispersive. The time taken for decapods, which are close to the top of the food chain, to respond to an increase in phytoplankton will be considerable. Assuming entrainment in the front and an average current of $10cms^{-1}$, >500 km could be covered in 2 months, nearly the same length of time taken to sample the five stations. The general trend of the front is NW to SE (Mann, 1967; Gould, 1985), it is very likely, therefore, that species of high abundance in the front (e.g. *Sergia japonicus* and *S. robustus* were advected from more productive areas to N.W.

Attempts to identify zoogeographical regions and to relate them to water masses have met with varying degrees of success and it is now clear that, whilst the distribution of many species can broadly be explained in these terms, the limits of species ranges rarely coincide exactly with physical boundaries. This present study is in agreement with this view as, the Azores Front which is a marked physical feature between distinct water masses, represents the boundary of only a few species. In terms of presence/ absence, therefore, there is little to distinguish the five decapod assemblages. However, a pattern does emerge from the comparison of ranked abundances which shows that the EAW and EAW eddy stations are closely linked while the WAW one stands apart.

The existence of structured pelagic communities that are distinct from one another has been questioned more than once (e.g. for Diatoms: Williams et al., 1981; and Fish: McKelvie, 1985). Differences in the environment on either side of the front will, not unnaturally, favour some species more than others and thus lead to differences in relative abundance, the significance of which are difficult to interpret. The study area is subject to quite pronounced mesoscale variability which is in addition to any seasonal influences and so it is likely that in the region of the front, at least, the relative abundances are in a state of constant flux.

The role of trophic relationships may well be very important (e.g. Pugh, this volume) although, as yet, they are only poorly understood for this region. In their study of thermal fronts Backus et al. (1969) postulated that some species of mesopelagic fish were particularly well adapted to areas of either high or low productivity, perhaps the same is true for other taxa. In the WAW, the lowest biomass was recorded in most other micronektonic and planktonic taxa as well as the decapods, this was most probably due to the low levels of primary productivity. The decapod fauna is especially lacking in detritivorous species. By this measure the WAW could be said to have a low productivity fauna, the fact still remains, however, that the species complement is substantially the same as the other four series, distinguished by the lack of some species rather than the addition of others.

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APPENDIX

Station	Position of centre		Dates 1981	Depth of the 16°C isotherm (in m)
10376 Frontal	33°20'N	33°20'W	26/5-30/5	295
10378 WAW Meander	32°20'N	29°50'W	7/6-10/6	254
10379 EAW	35°00'N	33°10'W	11/6-15/6	146
10380 WAW	30°00'N	33°50'W	16/6-20/6	318
10382 EAW Eddy	32°33'N	32°33'W	21/6-24/6	194

Abbreviations: EAW (Eastern Atlantic Water)
WAW (Western Atlantic Water)

THE PLEISTOCENE EQUATORIAL BARRIER BETWEEN THE INDIAN AND PACIFIC OCEANS AND A LIKELY CAUSE FOR WALLACE'S LINE

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Scripps Institution of Oceanography, U.S.A.

INTRODUCTION

Between Miocene and Pliocene time 15 to 5 million years ago, the Australian/New Guinea plate and the Asian plate collided (Audley-Charles et al., 1981; Audley-Charles, 1981) and established the contemporary alignment of land and sea in the Indo-Australian region. Subsequent eastward dispersal of some oriental terrestrial plants and animals and westward dispersal of some Australian / New Guinean terrestrial species across the collision boundary apparently failed. The imperfect dispersal of the two biotas became the basis for a series of proposed biogeographical boundaries (Fig. 1) that extend north to south across eastern Indonesian seas between the east coast of Borneo and the western end of Vogelkop Peninsula off western-most New Guinea (Carr, 1972; Raven & Axelrod, 1972; George, 1981). The extreme boundaries are Wallace's line lying east of the Philippines and passing south between Borneo and Celebes and Lydekker's line, a dogleg lying west of New Guinea and east of Ceram and the Kai and Tanimbar Islands. The two lines delineate an area of biotic transition between Asian and Australian/New Guinean faunas and floras some-

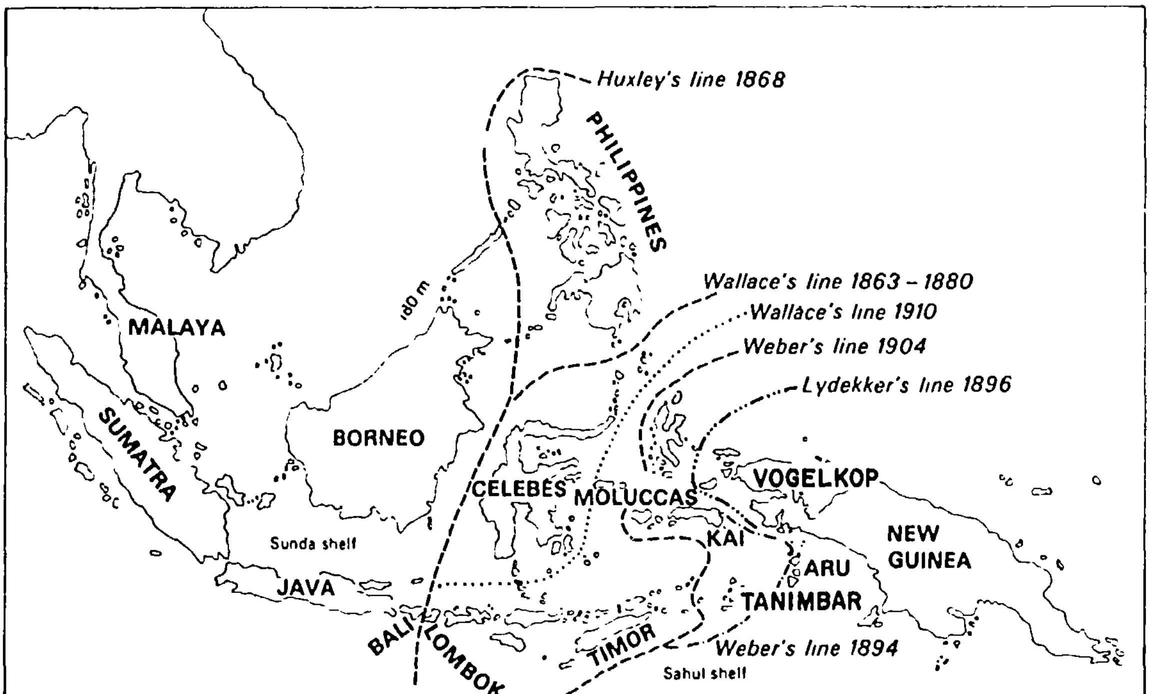


Fig. 1 Biogeographic boundaries proposed for separating the Oriental and the Australia/ New Guinea faunal regions. (cf. George, 1981).

times referred to as Wallacea (Mayr, 1944). Wallacea encompasses the eastern Indo- nesian seas, the major tropical seaway connecting the Indian and Pacific Oceans and the only tropical connection during Pleistocene glacial stages.

In this paper I consider several lines of evidence that Wallacea was the likely site of profound, vicariant events during Pleistocene glacial stages. These events influenced the distribution and speciation of pelagic, equatorial, Indo-Pacific stenothermal species inhabiting the mixed layer. Support for the hypothesis that Wallacea has been a geographical barrier during Pleistocene glacial stages derives from several sources:

1. Evidence of annual coastal wind driven upwelling off western New Guinea.
2. Presence of an upwelling species endemic to the Indo-Australian region, *Calanoides philippinensis*.
3. Estimates of reduced surface water temperatures in Pleistocene glacial periods.
4. Speciation patterns of pontellid copepods inhabiting surface waters of the Indo-Australian region.
5. Presence of an apparent hybrid zone across Wallacea in copepods of the genus *Undinula*.

UPWELLING OFF NEW GUINEA

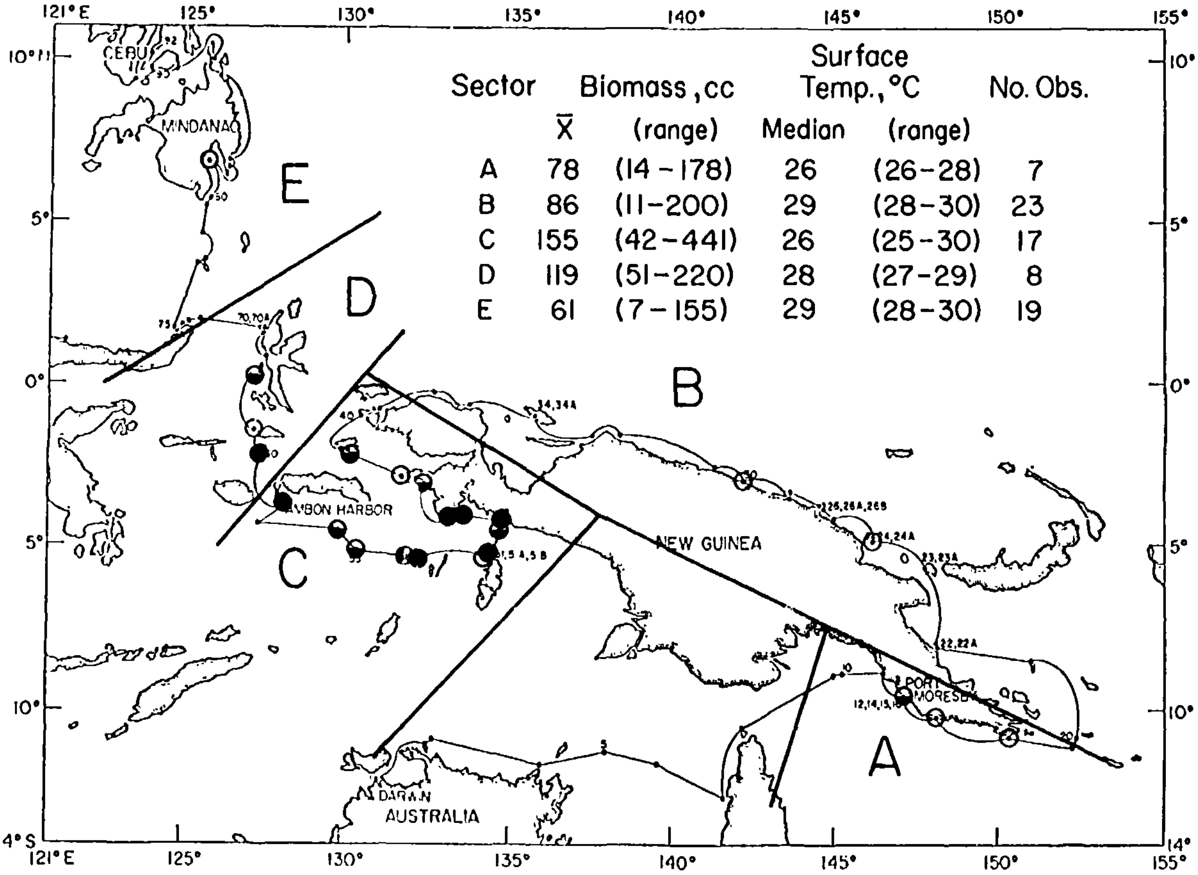
Upwelling in Wallacea first came to my attention in midyear of 1979, in the course of a biological collecting expedition aboard R/V Alpha Helix working coastal waters in eastern Indonesian seas. Figure 2 shows the track of the expedition.

To facilitate comparisons, the track has been divided arbitrarily into sectors labeled A, B, C, D & E. Median surface temperatures and mean zooplankton biomass, sector by sector, are shown in the table above the cruise track (Fig. 2). Circled stations had zooplankton biomass, measured as displacement volume, above 150cc per standard tow; half-filled and filled circles are stations at which upwelling species of copepods were collected.

Sector C showed the most pronounced effects of coastal upwelling. Surface temperatures were as low as 25°C, mean zooplankton biomass and the proportion of high biomass stations were the highest of the cruise, and almost all the samples contained upwelling species. Furthermore, the sector C samples contained few if any of the 40 stenothermal species of Pontellidae that were collected in the course of the expedition. High values in sector D appear to be the consequence of advection from sector C. Sector A also had low temperatures, few pontellids, and sufficient phytoplankton to discolor the net, but, in view of the low zooplankton biomass and the scarcity of upwelling copepods, the upwelling was clearly in an earlier phase of development. The cause of the upwelling appeared to be the SE Trade Winds blowing 15 to 25 knots, day and night, during this phase of the southern hemisphere winter.

A series of histograms (Fig. 3) allows one to compare surface temperatures with (1) biomass, (2) the occurrence of the upwelling copepods, *Calanoides philippinensis* and *Rhincalanus nasutus* and (3) the abundance of stenothermal copepods belonging to the family Pontellida. Station numbers are shown at the bottom of the figure. Samples were taken with a 1m plankton net fished horizontally at the surface for twenty minutes at dawn or dusk. Stations 40 to 60 located south and west of New Guinea produced the lowest temperatures, the highest biomass, the largest numbers of upwelling species, and the lowest abundance of stenothermal pontellids. Typical surface temperatures at coastal water stations, sampled at dawn and dusk, measured 28°C. At midday they tended to rise to 30°C. Minimum sea surface temperatures of 25°C were apparently depressed about 3°C by the upwelling.

Although phytoplankton biomass was not measured, it should be noted that stations producing high zooplankton biomass and low surface temperatures (<27°C) tended to have high quantities of phytoplankton contributing to the green, turbid qualities of the water observed at these localities. Furthermore, at these stations and many stations of sector A the zooplankton net usually came aboard coated with a thick green layer of phytoplankton. The highest concentrations of upwelling species, highest zooplankton biomass measurements, and the lowest temperatures occurred just west and north of the Aru Archipelago.



Sector	Biomass ,cc $\overline{X}$	Biomass ,cc (range)	Surface Temp.,°C Median	Surface Temp.,°C (range)	No. Obs.
A	78	(14 - 178)	26	(26-28)	7
B	86	(11-200)	29	(28-30)	23
C	155	(42-441)	26	(25-30)	17
D	119	(51-220)	28	(27-29)	8
E	61	(7 - 155)	29	(28-30)	19

Fig. 2 Cruise track, Moro Expedition 31 May to 24 July 1979, aboard RV "Alpha Helix". 1m net, 505 mesh, towed at surface for 20 minutes at dawn or dusk at numbered stations. Biomass, measured and reported as displacement volume per 20-minute surface tow, exceeded 150cc at stations marked by a circle. Circles half filled and filled also indicate presence of one or two upwelling species of copepod, respectively. Sectors A to E, determined arbitrarily, provide means for highlighting area of low surface temperature, high biomass and frequent occurrence of upwelling copepods.

COPEPOD UPWELLING SPECIES IN THE INDO-AUSTRALIAN REGION

Biogeographically, the two upwelling species are very different. *Rhincalanus nasutus* appears to be circumglobal and occurs primarily in temperate boundary currents and in tropical upwelling. My unpublished data on Calanidae which include a cladistic analysis of phylogeny and a biogeographic study of *Calanoides* supports the hypothesis that *C.philippinensis* evolved relatively recently within the Indo-Australian region and probably at a time when upwelling was much more widespread in this region. Most Indo-Malayan records of *R.nasutus* and *C.philippinensis* taken by the two previous expeditions in Indonesian waters, Siboga (Scott, 1909) and Snellius (Vervoort, 1946), were also obtained from west and south of New Guinea (Fig. 4). I have also found *C.philippinensis* in this region in surface collections taken off southwest New Guinea in midyear, 1976 and 1977, by an SIO expedition called INDOPAC. Thus, there is ample reason to accept two facts with significant historical implications for Wallacea. 1. Upwelling is an annual midyear event in the southern hemisphere

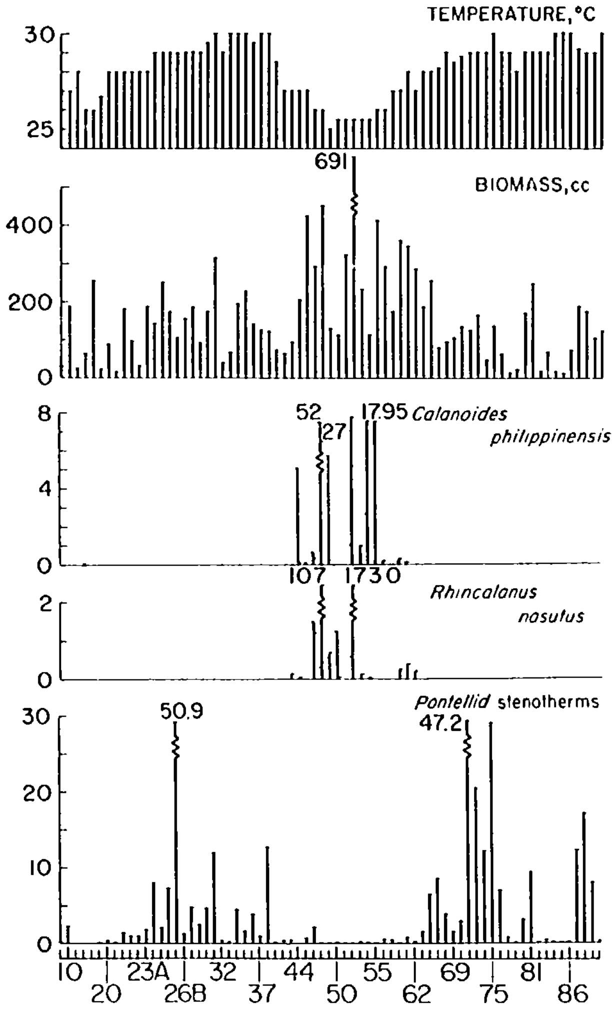


Fig. 3 Moro Expedition, 31 May to 24 July 1979. Histograms of temperature, biomass (cc) as displacement volume per 20-minute surface tow, abundance of upwelling species, *Calanoides philippinensis* and *Rhincalanus nasutus*, no. adults/m^3 shown by tick to left of vertical line, no. juveniles/m^3 shown by tick to right of vertical line; lowermost histogram shows sum total of stenothermal species of copepod family Pontellidae represented in samples of expedition by 15 species of *Pontella*, 14 species of *Labidocera* and 11 species of *Pontellopsis*. Station numbers shown on scale at bottom; stations 40 to 60 with lowest temperatures, highest biomass, largest numbers of upwelling species and lowest numbers of stenothermal pontellids. Subsamples were obtained with the aid of a Folsom plankton splitter for large, highly varied samples and a Stempel pipette for small samples dominated by copepods. Counts, usually based upon microscopic examination of 5% of the total sample, the range varying from 2% to 10%.

winter prompted by the winter-intensified SE Trade Winds.

2. *Calanoides philippinensis* appears to have evolved in the vicinity of Wallacea and probably during a period when the cool water conditions, and the dense phytoplankton populations it favours, were much more extensive than they are now. Compared to the huge populations of its congeners off Africa, South America, South Australia and the Antarctic, *C. philippinensis* appears to be barely surviving at present.

Extrapolating from available sampling records (Figs 3, 4)(deep tows from Siboga and Snellius Expeditions produced only late copepodites, surface tows in winter months from Moro and INDOPAC Expeditions produced adults and young copepodites), *C. philippinensis* appears to behave as do its allopatric congeners. They tend to enter the mixed layer during seasonal periods of enrichment where they mature and reproduce. Late immature individuals (i.e. stage V copepodids) of the next or some subsequent generation store large quantities of lipids. They leave the mixed layer apparently when food supplies decline precipitously (Smith, 1982) to enter diapause at about 300 to 500m or deeper. The diapausing stocks remain as late juveniles at depth until the onset of the next upwelling period as described for *Calanoides carinatus* and *Calanus pacificus californicus* (Binet & Suisse de Saint Claire, 1975; Petit & Courties, 1976; Alldredge et al., 1984).

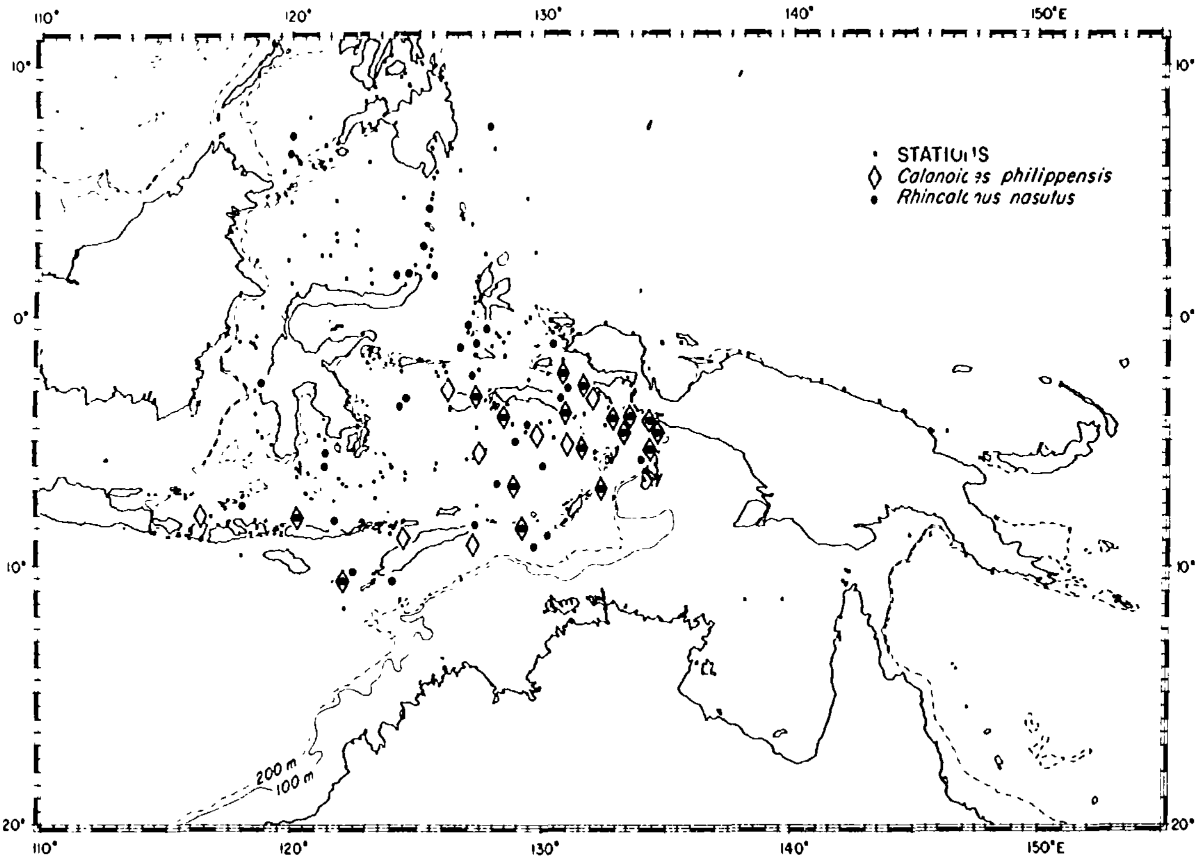


Fig. 4 Composite stations of the Siboga Expedition (1899), the Snellius Expedition (1929) and R/V "Alpha Helix" Moro Expedition (1979). Stations are indicated by small filled circles, *Calanoides* records by open diamonds, and *Rhincalanus* records by a large filled circle. Note how positive records are concentrated off southwestern New Guinea.

SURFACE TEMPERATURES DURING PLEISTOCENE GLACIAL STAGES

Figure 5 considers Indo-Australian sea surface temperatures in the present interglacial and estimated temperatures prevailing during Pleistocene glacial stages. General features of figure 5 are from Webster & Streten (1972) and the CLIMAP Project (1976). Neither source, however, allows for the influence of coastal upwelling.

The top two panels in figure 5 show present conditions prevailing in the two halves of the year. The bottom two panels approximate conditions thought to exist during Pleistocene glacial stages, when sea level was lowered by 100 to 200m. Dotted shading in the area of Wallacea represents special local conditions that would have lowered surface temperatures on a seasonal basis.

Quinn (1971) argues for increased upwelling in equatorial latitudes of the westernmost Pacific during Pleistocene glacial stages. He notes the existence of fossil guano deposits on equatorial islands lying west of the Gilberts, which indicates the past presence of large colonies of sea birds on islands now lacking such colonies. Presumably during Pleistocene glacial periods, equatorial upwelling in the West Pacific provided the resources to support the now extinct bird

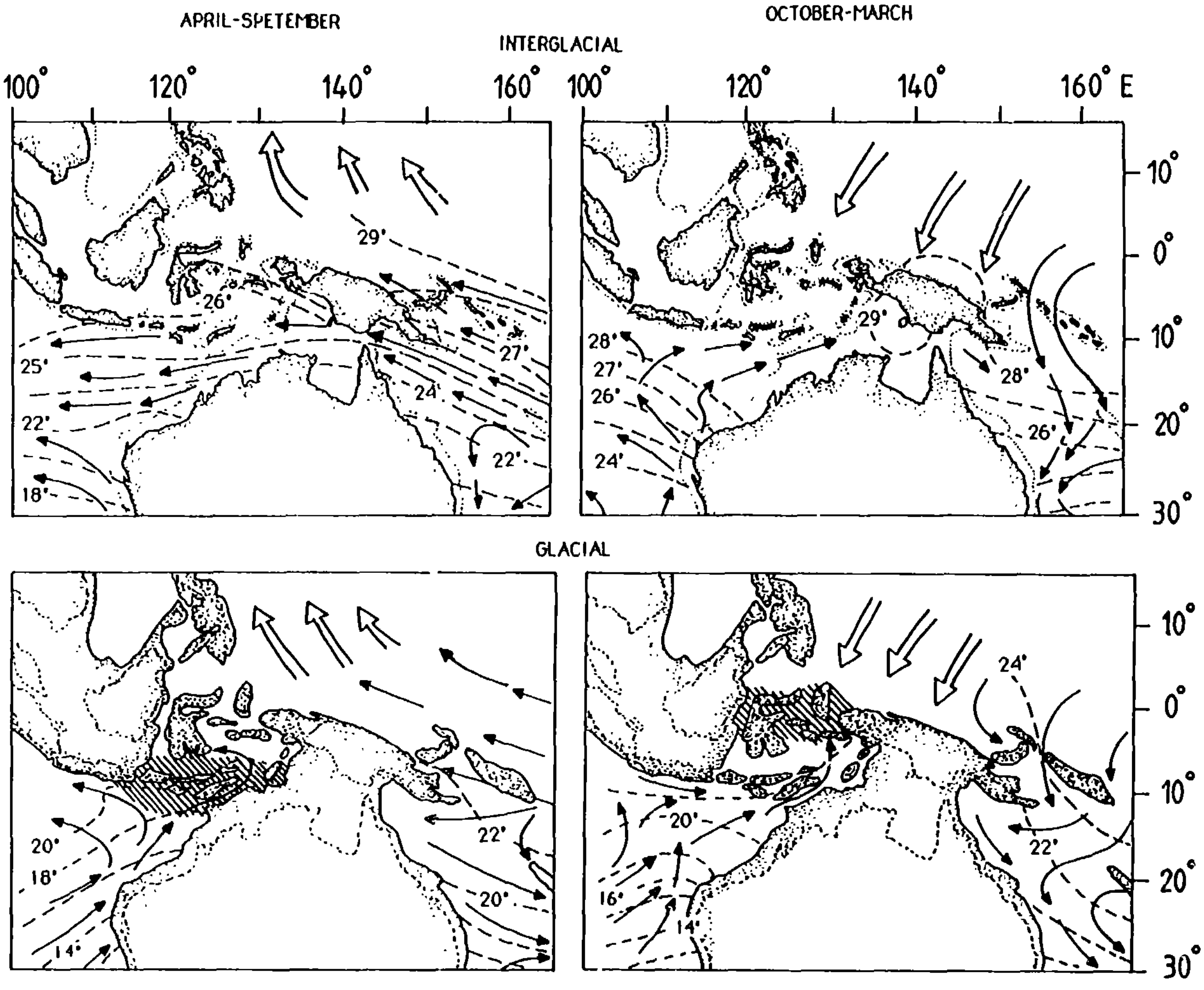


Fig. 5 Sea surface temperature isotherms, °C, surface currents (slender arrows) and Northeast Trade Winds (thick arrows) in eastern Indo-Australian region. Top two panels show conditions in southern hemisphere winter and summer conditions in the present time and hypothesized for past interglacial stages. Bottom two panels show conditions thought to prevail during Pleistocene glacial stages. Oblique line shading in bottom two panels show areas in which unusually cool (<21°C) surface temperatures may have predominated seasonally and acted as a barrier to the passage of mixed layer stenotherms; land area extended to 200m isobath to approximately lowered eustatic sea level during glacial stages. (modified from Webster& Streten, 1972; Brinton,1975).

colonies. In general over the past 75000 years, fluctuations in the intensity of the trade winds has been concurrent or preceded fluctuations in the amount of ice stored on continents and wind velocity of the winter trades intensified during cool climatic stages of the earth and diminished during warm stages (Molina-Cruz, 1977). Pleistocene glacial stages appear to have persisted for periods of tens of thousands of years. Bé & Duplessey (1976) show that the half-million-year record for the western Indian Ocean and the quarter-million-year record for the eastern Indian Ocean had cold conditions prevailing for more than half of their respective periods. Van Andel et al. (1967) and Webster & Streten (1972) believe that cool water entered the Timor Sea during Pleistocene glacial stages based on an intensification of the cool, west Australian boundary current and its more northward penetration. Changes in current intensity during Pleistocene glacial stages have been recorded off South Africa (Hutson, 1980).

In the northern hemisphere during Pleistocene glacial winters, the NE Trades probably intensified sufficiently to induce coastal upwelling off northwest New Guinea and the eastern Moluccas. Webster & Streten (1972) suggest that surface temperatures off northwest New Guinea ranged from 22 to 24°C, while the CLIMAP Project (1976) indicates 25 to 27°C in the southern hemisphere winter for this area. Reducing these values by 3°C, the extent surface temperatures are lowered in upwelling plumes off New Guinea, would depress winter Pleistocene surface temperatures to a range of 19 to 24°C, i.e., well below present-day winter conditions. Assuming that the median, 21.5°C, is close to actual surface temperatures in upwelling plumes of the Pleistocene glacial winter, the northern end of Wallacea would be inhospitable to tropical stenotherms roughly from October to March. In the southern hemisphere's winter, the West Australia Boundary Current would intensify and the SE Trades might cause coastal upwelling along the Sahul shelf. It is reasonable to expect winter surface temperatures of about 20°C in the Timor and Banda Seas, as shown by Webster & Streten (1972), rendering the southern end of Wallacea inhospitable to surface-bound stenotherms roughly between April and September.

The hypothesized glacial-stage conditions shown in the lower two panels of figure 5 would enhance *C.philippinensis* and *R.nasutus* population expansions, while depressing populations of stenothermal pontellids. Stratigraphic evidence by Bé & Duplessy (1976) indicates that the glacial stages persisted for tens of thousands of years several times during the million years of the Pleistocene. For stenothermal species ranging across Wallacea, each glacial sequence would interrupt their distribution and provide an opportunity for the allopatric subpopulations to diverge.

PONTELLID SPECIATION PATTERNS

If Wallacea was a long-term barrier to passage of stenothermal species of the mixed layer, we should expect to see evidence of its vicariant role in speciation patterns of locally distributed species groups. That is, sister species may be expected to have allopatric or parapatric distributions extending from Wallacea.

Pontellid copepods are abundant and species rich in the Indo-Australian region. I have recorded to date 69 species in the three principal genera, *Labidocera, Pontella* and *Pontellopsis,* 48 being endemic to the region. Most are or appear to be stenothermal, and all live in the upper few meters of the mixed layer. Up to now I have examined the systematics and distribution of five species groups of these pontellids. With few exceptions, these species are short ranging and inhabit coastal or neritic waters. I have assumed from their morphologic and geographic relationships that allopatric speciation is the principal, and likely the sole, process of cladogenesis in this family. Hypothesized phylogenetic relationships for each group based on sexually modified apomorphies are shown in figure 6. Circled nodes represent hypothesized speciation events that appear, on the basis of present distributions, to have occurred in the vicinity of Wallacea. Every group has at least one apparent speciation event associated with Wallacea. About 30% of cladogenesis in the five groups appears to indicate a past Wallacean barrier.

The lack of a fossil history precludes direct dating of copepod speciation events. However, two sources of inferential evidence provide a yardstick for estimating speciation rates in coastal to slope-water copepods. One source is a study of geographical variation in *Calanus helgolandicus* s.l. (Fleminger & Hulsemann, unpubl.). The second (Fleminger, 1975) is from speciation patterns in American lineages of *Labidocera*. *C.helgolandicus* s.l. in the Black Sea has diverged behaviourally and morphologically from the Mediterranean ancestor and appears to have induced reinforcement of reproductive barriers in the Aegean and Adriatic populations. The Black Sea has had a complex

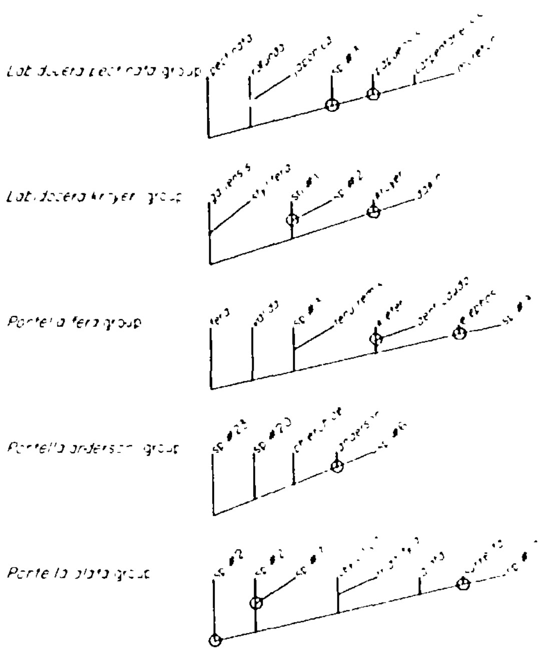


Fig. 6 Cladograms showing hypothesized phylogenetic relationships in pontellid copepod species groups indigenous to the Indo-Australian region. Circled nodes represent hypothesized speciation events that appear on the basis of present distributions to have occurred in the vicinity of Wallacea. Cladistic analyses based on sexually modified morphology. Species indicated by number are undescribed.

history varying through Pleistocene time from brackish marine to freshwater-brackish (Caspers, 1957). When the Black Sea assumed its present marine-brackish quality to support a *Calanus* population is not established. Nevertheless, *Calanus* could not have survived the freshening at the beginning of Würm 100,000 years ago. Indeed, the most recent successful colonization from the Sea of Marmara may have begun after the end of the most recent glaciation, less than 12,000 years ago.

Labidocera in the Americas is represented by 18 species divided among four distinctively different species-groups (Fleminger, 1975). Two groups are restricted to Atlantic-Caribbean coastal-neritic waters and two to Pacific coastal-neritic waters. The species have relatively restricted geographical ranges (i.e., short-ranged) and tropical or subtropical temperature requirements. Their present distribution relative to closure of the Isthmus of Panama about 3,5 million years ago (Woodring, 1966) suggests that these species groups, virtually the equivalent of genera in better-studied taxa, may have evolved in less than 3.5 million years. This is similar in duration to more familiar estimates of rapidly evolving genera. For example, all evolution in the Galapagos Islands, including radiation of 13 species of Darwin's finches, occured within 3 to 4 million years (Hickman & Lipps, 1985). Thus the *Calanus* and *Labidocera* data suggest speciation rates falling between 10^6 and 10^4 years.

The geographical distribution of each of these five groups are sufficiently similar that anyone can serve as an example of the others. Figure 7 shows the distribution of the *Labidocera pectinata* group (Fleminger et al., 1982). It is the most coastal of the five groups, typically being confined to waters inshore of the 100m isobath. The extent of shading offshore in the figure is, in most cases, merely for illustrative purposes, and not intented to depict the actual offshore distribution of individual species. Two sets of sister species converge on Wallacea, *L.papuenis* and *L.carpentariensis,* north and south relative to Wallacea, and species #3 and *L.carpentariensis*, east and west of Wallacea. A prolonged temperature barrier in Wallacea would have divided a continuous population into two or more allopatric subpopulations. Similar observations can be made for the other four pontellid species groups that have been studied.

Considering the sequence of Pleistocene glacials and interglacials, reduction of eustatic sea level by about 200m, and surface cooling by coastal upwelling, the history of the *Labidocera pectinata* group may have been roughly as hypothesized in figures 8 A-D. Accepting that the cold, surface-water barrier in Wallacea, as discussed above, persisted for thousands to tens of thousands of years, the opportunity did exist for speciation of the isolated populations.

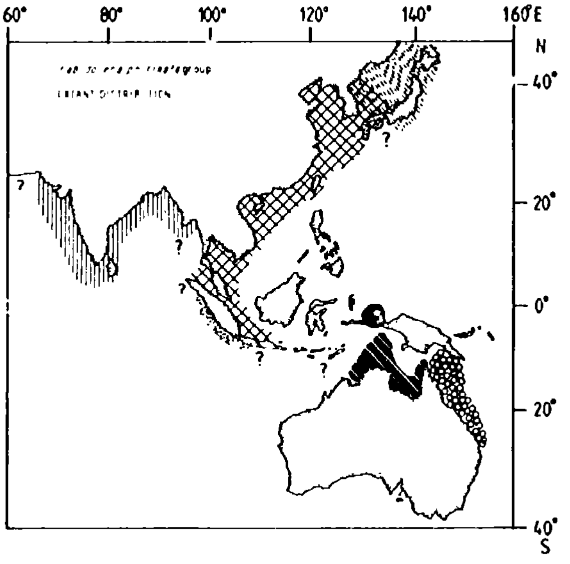
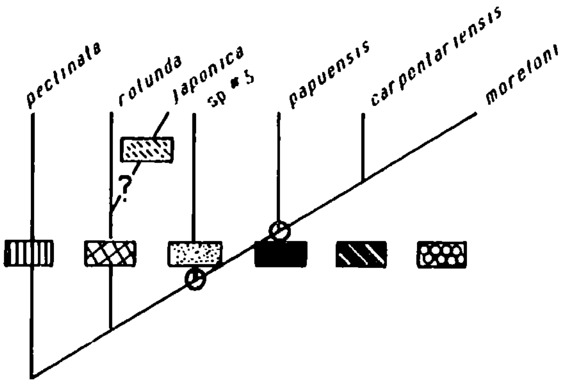


Fig. 7 Present geographical distribution of the *Labidocera pectinata* species group, based on localities cited in Fleminger et al. (1982) and new unpublished data. Extent of shading offshore is merely for illustrative purposes and not intended to depict actual offshore distribution of individual species; in most cases offshore distribution is confined to waters inshore of the 100m isobath. Cladogram in lower left shows hypothesized phylogenetic relationships of species and shadings representing ranges of individual species. Circled nodes are hypothesized speciation events that appear to have occurred in the vicinity of Wallacea.



UNDINULA HYBRID ZONE IN WALLACEA

Undinula vulgaris is a species complex within the family Calanidae that has a *Calanus*-like role, ecologically, in equatorial neritic waters circumglobally. The systematics of *Undinula vulgaris* s.l. at the species level are largely incomplete. Preliminary studies by Vervoort (1946) that were expanded by an unpublished study of Fleminger & Hulsemann indicate a zone of high variability in *U. vulgaris* in the area of Wallacea.

Three subspecific forms of *Undinula vulgaris* s.l. have been recognized in the Indo-Pacific: 1. *U. v. zeylanica* inhabiting coastal waters around oceanic islands; 2. *U. v. typica* occurring in continental neritic waters in the East Pacific, off Asia, and East Africa; and 3. *U. v. giesbrechti*, a variable population largely concentrated in Wallacea and more or less intermediate to *U. v. zeylanica* and *U. v. typica*. These trinomen are current in the copepod literature and are retained in the present paper since it is not a suitable vehicle to propose nomenclatoral changes.

Figure 9 is a preliminary summary of three female sexual characters that differ in the three forms. The scatterdiagram shows the distribution of one varying character, the length of the right side of the last thoraric segment, plotted against standard (prosome) body length. The two topmost clusters of open squares and crosses represent *U. v. zeylanica* from the Marshalls and Samoa. The cluster of open circles below represent *typica*, the continental form from Indian and East Pacific coastal localities. The intermediate *U. v. giesbrechti* is represented by filled squares, filled circles, and filled triangles lying intermediate to *U. v. typica* and *U. v. zeylanica*. The Atlantic population also assigned to *U. v. typica* by previous authors, though in error in my judgement, is represented by the open, inverted triangles below.

The drawings on the left depict the adult female right fifth pediger-bearing thoracic segment, and the distribution of cuticular glands associated with one of the sites on which the male spermatophore is cemented. *U. v. zeylanica* at the top left has columnar cells arranged perpendicular to the articulation with the fourth pediger-bearing thoracic segment. *U. v. giesbrechti*, second from the top, has numerous

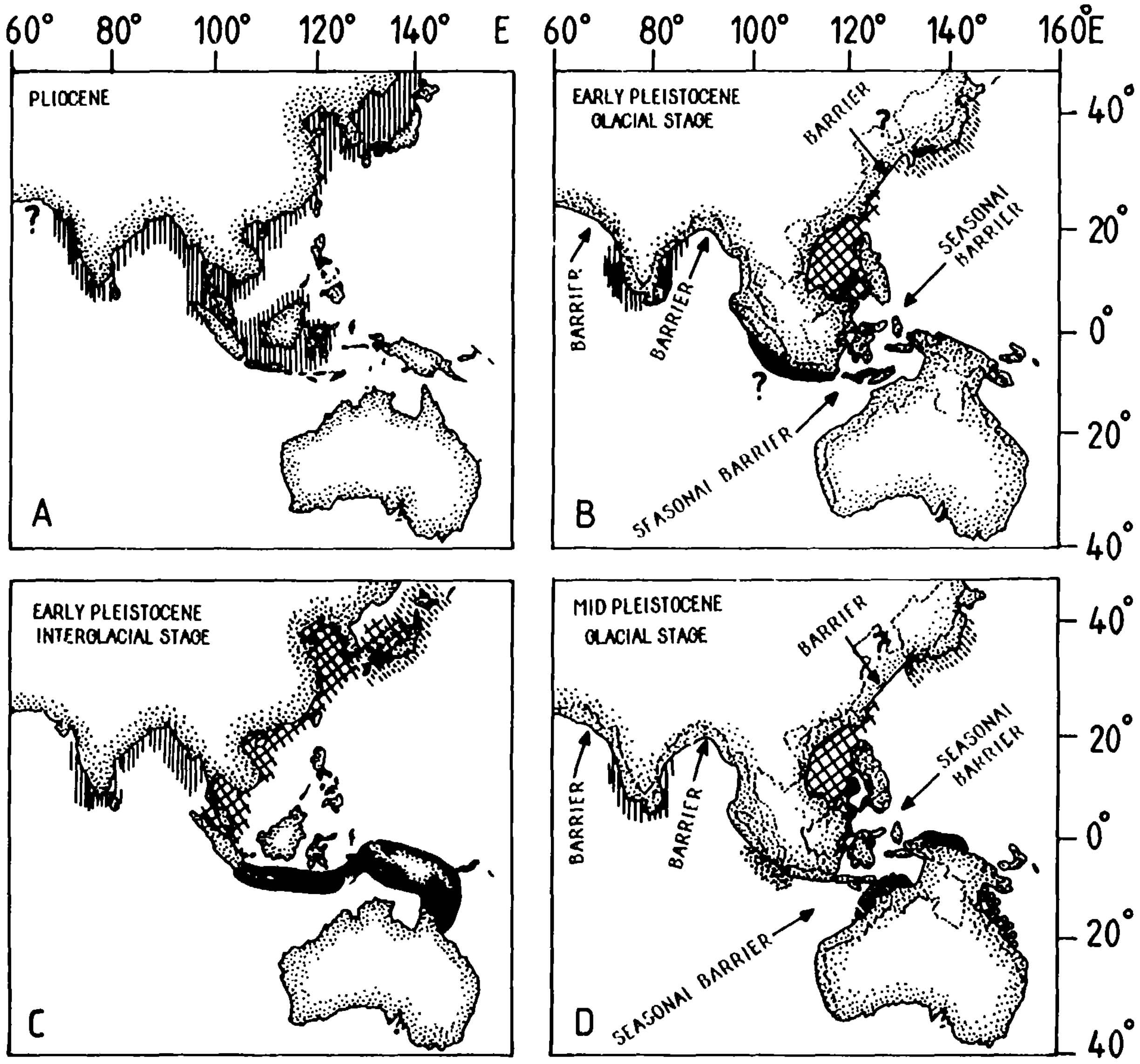


Fig. 8 Hypothesized sequence of speciation in the *Labidocera pectinata* group. Continental barriers are based on major land drainage systems that would interrupt distributions of coastal water species during glacial stages and melt periods leading into an interglacial stage. Seasonal barriers refer to the cooling effects of probable seasonal upwelling during the northern hemisphere winter and the cooling effects of the West Australia Boundary Current, as well as possible coastal upwelling in the southern hemisphere winter as discussed in the text. Shadings are identified in figure 7, except that the vertical lines in panel A refer to an ancestral precursor of *L. pectinata*.

glands scattered across both the fourth and fifth pediger-bearing thoracic segments. Indo-Pacific *U. v. typica*, third from the top, has a few glands scattered over the fifth pediger-bearing segment. The Atlantic form of *U. v. typica*, bottom left, has columnar glands distributed along the dorsal border of the fifth pediger-bearing segment. The smaller figures on the right show the fifth pediger-bearing thoracic segment and genital segment in the left lateral and dorsal views, *U. v. zeylanica* at the top, *U. v. giesbrechti* in the middle, and the Indo-Pacific *U. v. typica* below.

It is tempting to regard *U. v. giesbrechti* as a hybrid population, the consequence of secondary contact between the oceanic *U. v. zeylanica* transported westward by the North and South Equatorial Currents and the Asian *U. v. typica*. In Wallacea, hybridization between *U. v. typica* and *U. v. zeylanica* probably would have spread after warming of surface waters in the present interglacial period.

DISCUSSION AND CONCLUSION

To summarize, Wallacea, the Pacific-Indian tropical seaway lying between Celebes and New Guinea, was greatly reduced in area during Pleistocene glacial stages when eustatic sea level fell 100 to 200m. Coastal upwelling prevalent today in highly localized areas off western New Guinea was probably more extensive during Pleistocene glacial stages and apparently provided conditions suitable for the evolution of an endemic upwelling species of *Calanoides*. Paleo-temperature estimates of surface waters in the glacial stages modified by likely upwelling effects suggests a low of about 21°C in the northern half of Wallacea during the northern hemisphere winter and about 20°C in the southern half of Wallacea during the southern hemisphere winter. Stratigraphic evidence indicates that these glacial stages persisted for as long as tens of thousands of years.

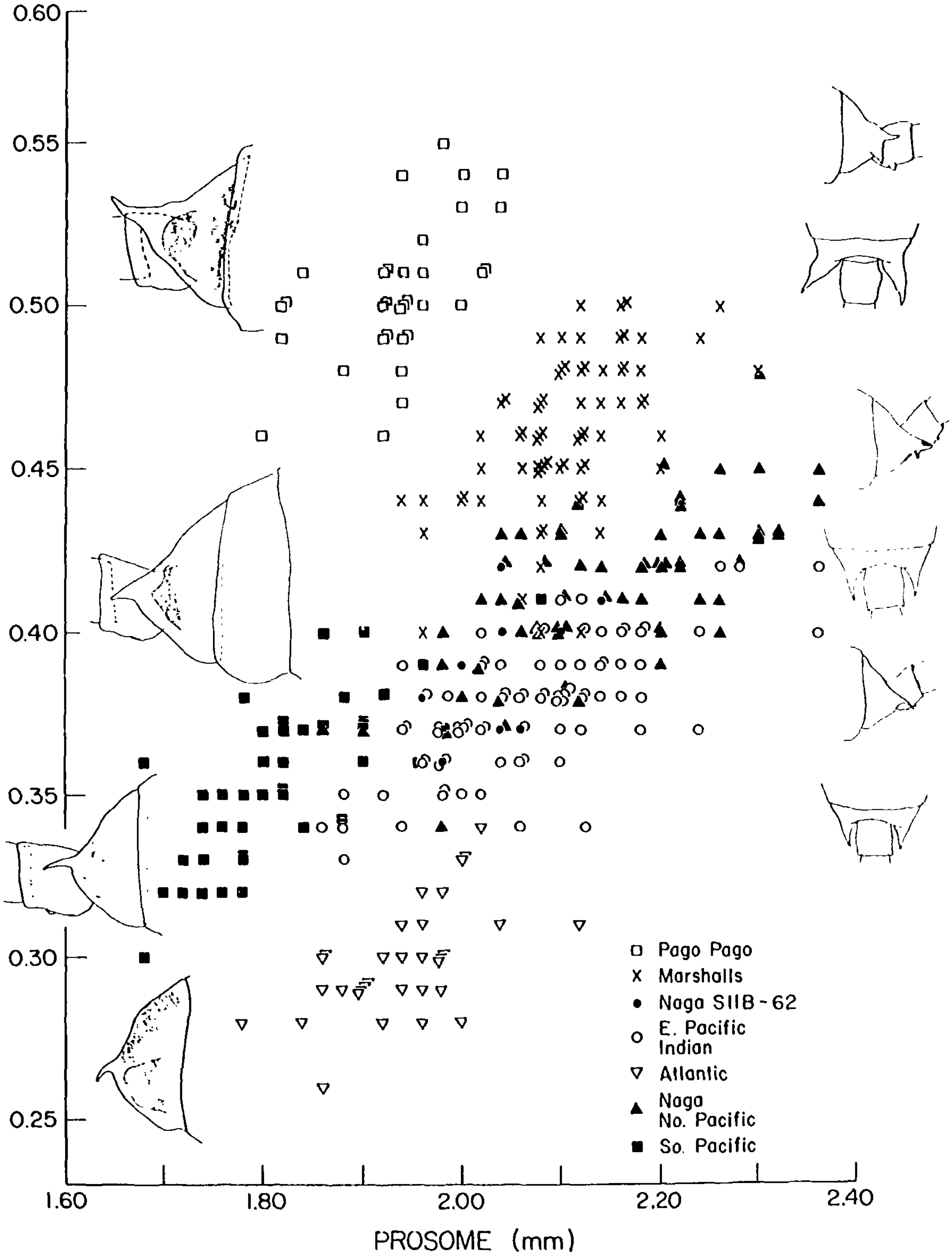
Five pontellid species groups show speciation patterns suggesting that Wallacea constituted a geographic barrier in the course of their cladogenesis. The barrier is conceived in terms of extensive chilling of Wallacean surface waters during Pleistocene glacial stages and is based on the avoidance of upwelling plumes by present-day stenothermal pontellids.

Further biological evidence is provided by the apparent hybrid swarm of *Undinula* in Wallacea. Though the *Undinula* study would benefit from additional data that may suggest an interpretation other than the one suggested above, the available results provide noteworthy support for the Wallacea hypothesis. This singular example of an east-west gradient of morphological change in sexually modified characters centers directly on Wallacea. Moreover, similar patterns of morphological diversity have not been observed elsewhere in *Undinula* or in any other genus of calanoid copepods.

Biological evidence is also provided by the otherwise unexplained failure of many lowland terrestrial plant and animal species to disperse across Wallacea either from Asia eastward or from Australia / New Guinea westward, the original basis for proposing the biogeographical boundaries between Borneo and New Guinea.

This hypothesized Wallacean barrier completes the sequence of geographical barriers in equatorial latitudes that began in Miocene-Pliocene time to interrupt Tethyan pelagic distributions and generate the present-day biogeographic patterns of equatorial pelagic species of the mixed layer. The Wallacea barrier hypothesis may be tested by stratigraphic studies in eastern Indonesian seas, and by feeding,

Fig. 9 *Undinula vulgaris* s.l., adult female. Scatter diagram showing length of the right fifth pediger-bearing thoracic segment (ThV) plotted against standard body length (prosome) in six geographical populations. Open squares and crosses represent subspecies *zeylanica* from Pago Pago and the Marshall Islands, respectively. Filled triangles, filled circles and filled squares represent subspecies *giesbrechti* from Wallacea north and south of equator, respectively. Open circles represent subspecies *typica* from Indian Ocean and eastern Pacific. Inverted open triangles represent subspecies *typica* from Atlantic Ocean. Small figures on the left are right lateral views of ThV and genital segment; distribution of cuticular glands and openings shown as columnar structures and dots. Shaded area indicates storage of glandular products. Small figures on right are left lateral and dorsal views of ThV and genital segment. From the top down, subspecies *zeylanica*, *giesbrechti* and *typica*; the fourth figure down on the left is subspecies *typica* from the Atlantic.


0.60
0.55
0.50
0.45
0.40
0.35
0.30
0.25
RIGHT Th V (mm)
1.60
1.80
2.00
2.20
2.40
PROSOME (mm)
□ Pago Pago
X Marshalls
● Naga SIIB-62
○ E. Pacific Indian
▽ Atlantic
▲ Naga No. Pacific
■ So. Pacific

reproductive and growth studies of pontellid stenotherms at temperatures ranging below 26°C. The evolution of tropical copepods species that have been analyzed in detail, i.e., the genera *Clausocalanus, Eucalanus,* selected species of *Centropages* and *Temora, Pontellina,* Calanidae, and the pontellid genera *Pontella, Pontellopsis* and *Labidocera* (Frost & Fleminger, 1968; Fleminger, 1973; Fleminger & Hulsemann, 1973, 1974; Fleminger, 1975 and unpublished) may be understood in the context of these low-latitude barriers interrupting the Tethyan Sea, i.e., the Panamanian Isthmus, the juncture of Asia Minor and northeast Africa, and Wallacea. These examples also emphasize the likelyhood that speciation in mixed-layer calanoid copepods can be accounted for by conventional geographical speciation processes.

ACKNOWLEDGEMENTS

The Wallacea barrier hypothesis derives primarily from zooplankton studies carried out in eastern Malesian coastal waters aboard R/V "Alpha Helix" during Moro Expedition. The zooplankton results from Moro Expedition provided much of the biotic and geographical perspectives needed to formulate the hypothesis. I am indebted to the National Science Foundation's "Alpha Helix" Program for the generous grant of ship time that permitted me to occupy 100 stations in the course of 6000-mile cruise track. I thank Frank Ferrari, who collaborated with me in sampling zooplankton, and my other shipboard colleagues, Frank Barnwell, Mark Bartness, John Boaz, Bruce Collette, Gordon Hendler, Geerat Vermeij and Elizabeth Zipser Vermeij, as well as national observers J.Munro and J.Pernetta (Papua, New Guinea), O.Kurnaen and A.Sutomo (Indonesia), and R.Estudillo and A.Olandez (Philippine Islands) for their kind cooperation. This paper is a contribution from the Marine Life Research Program of Scripps Institution of Oceanography.

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THE STOMIOID FISH GENUS EUSTOMIAS AND THE OCEANIC SPECIES CONCEPT

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INTRODUCTION

We cannot study biogeography, even in the simplest way, unless we know what species we are working with. It is even better, of course, if we know their phylogenetic relationships. It is my contention that we are a long way from knowing what species really exist in the oceanic environment. Workers are taking existing taxonomic works for granted, and this is a mistake. We must look harder at the organisms that we work with, examine more characters, and make an attempt to recognize the several species that so often are hiding under a single name. There are more species out there than we realize.

THE GENUS EUSTOMIAS

I will illustrate my point by a consideration of the mesopelagic, predatory fishes of the genus *Eustomias*. The species of *Eustomias* are seldom taken in numbers in the gear most commonly used for sampling the oceanic mid-waters, and it has taken a long time to obtain series that are sufficient to show variation or consistency in morphological characters. As it turns out, while groups within *Eustomias* can be recognized by a number of different kinds of characters, the species within these groups are recognized almost entirely by the structure of the barbel that hangs from their chin.

In the 45 years from 1888, when the genus and first species were described, until 1933, 64 nominal species of *Eustomias* were described, all of them from the Atlantic. Then, in 1939, Beebe & Crane questioned the validity of a number of the species and reduced several of them into synonymy. I followed suit in 1964, not believing that so many minor variations in barbel structure could indicate species status, and I recognized as valid only 37 of the 66 names that had been decribed (Morrow & Gibbs, 1964). It would seem that workers were convinced that it was unwise to describe new species, for in the 50 years from 1933 to 1983 only ten were described, all from the Indo-Pacific and all valid.

In 1983 the bubble burst when the first of a series of papers was published by myself and co-workers based on our realization that the conservative approach had been wrong. In one subgenus, *Nominostomias*, where eight species previously had been recognized as valid, we restored five species from synonymy and described 25 new ones (Gibbs, Clarke & Gomon, 1983). Papers now in press or contemplated soon will bring the number of *Eustomias* species to well over a hundred.

What has happened is that subtle differences that we once believed were variations in a single species are being found to be repeated, to occur in both sexes, and to have geographic integrity. Figure 1 shows the barbels of four Atlantic and six Pacific species of *Nominostomias*, all of which have two terminal bulbs and a single, simple terminal filament. In 1964, I would have recognized these as only one species (*N. bibulbosus*), sceptical that such minor differences could be more than intraspecific variation. Five more species, three Atlantic and two Pacific, of the same subgenus are shown in figure 2. These also have a single central filament, but with side branches well developed. In 1964 I considered them to be the same species (*N. bibulbosus*) as the previous ten. A third group of two-bulbed species is shown in figure 3. These have several filaments arising together from the terminal bulb. I considered the two described Atlantic species to be one in 1964. Now we recognize three Atlantic and five Indo-Pacific species, and one that occurs in both the Atlantic and the Indo-Pacific, the only species in the subgenus to do so. Thus,

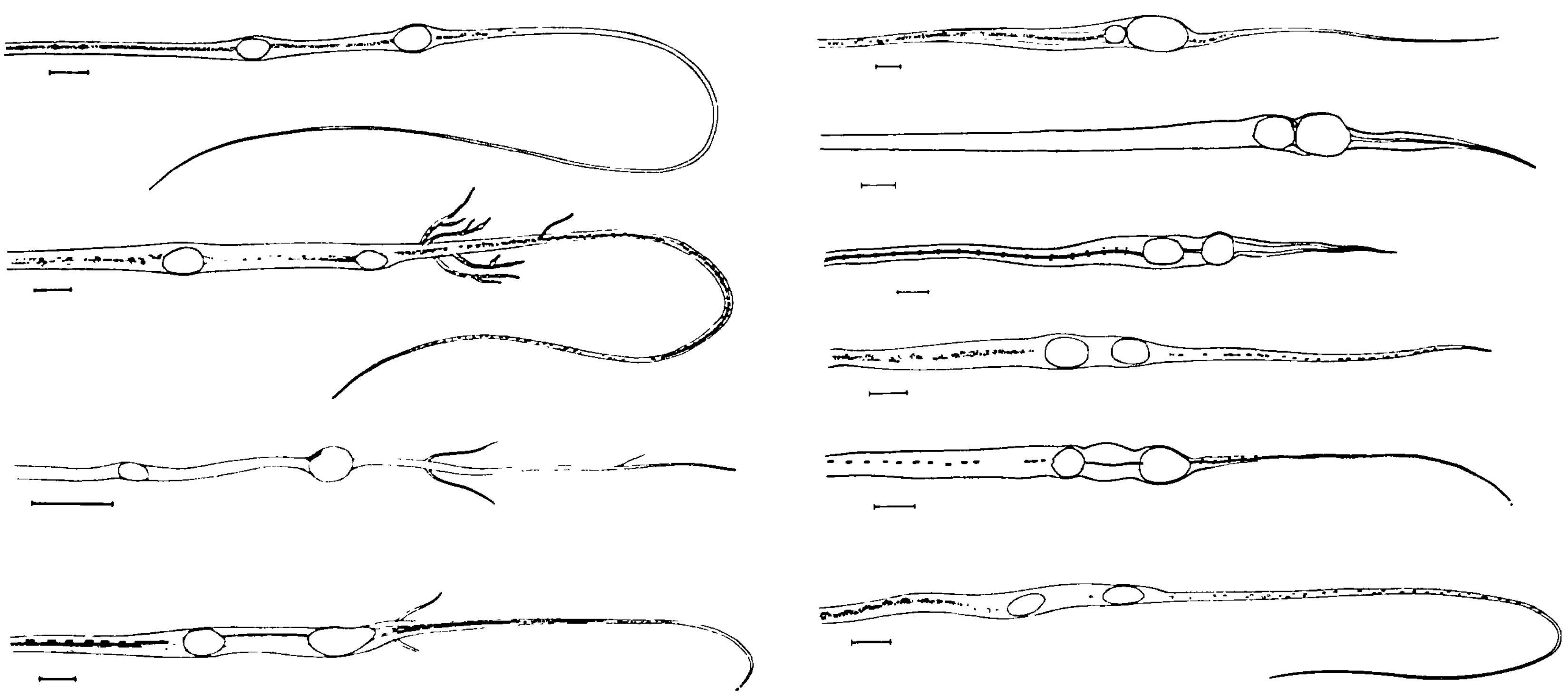

Fig. 1 Barbels of *Eustomias* (*Nominostomias*) species with simple terminal filaments. Left, Atlantic species -- top to bottom: *E. bibulbosus*, *E. micraster*, *E. australlanticus*, *E. bituberatus*. Right, Pacific species -- top to bottom: *E. inconstans*, *E. appositus*, *E. orientalis*, *E. bibulboides*, *E. australensis*, *E. bituberoides*.

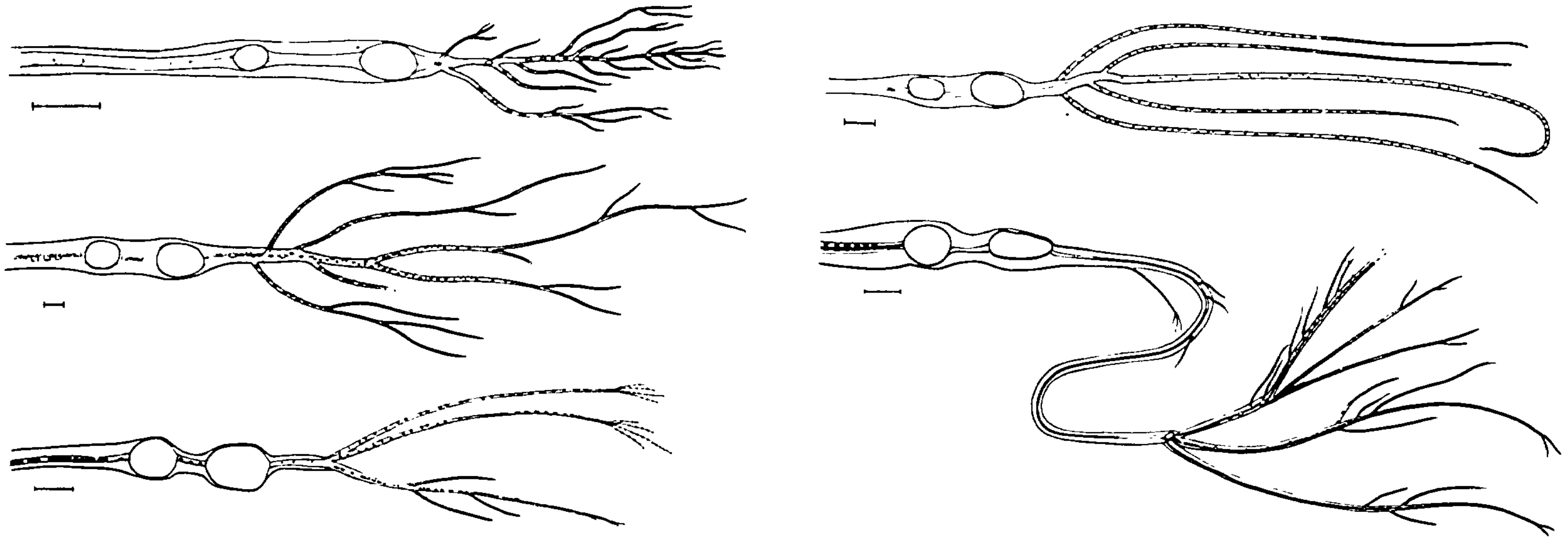

Fig. 2 Barbels of *Eustomias* (*Nominostomias*) species with branches from a central filament. Left, Atlantic species -- top to bottom: *E. arborifer*, *E. grandibulbus*, *E. bimargaritatus*. Right: Indo-Pacific species -- upper, *E. crossotus*; lower, *E. bimargaritoides*.

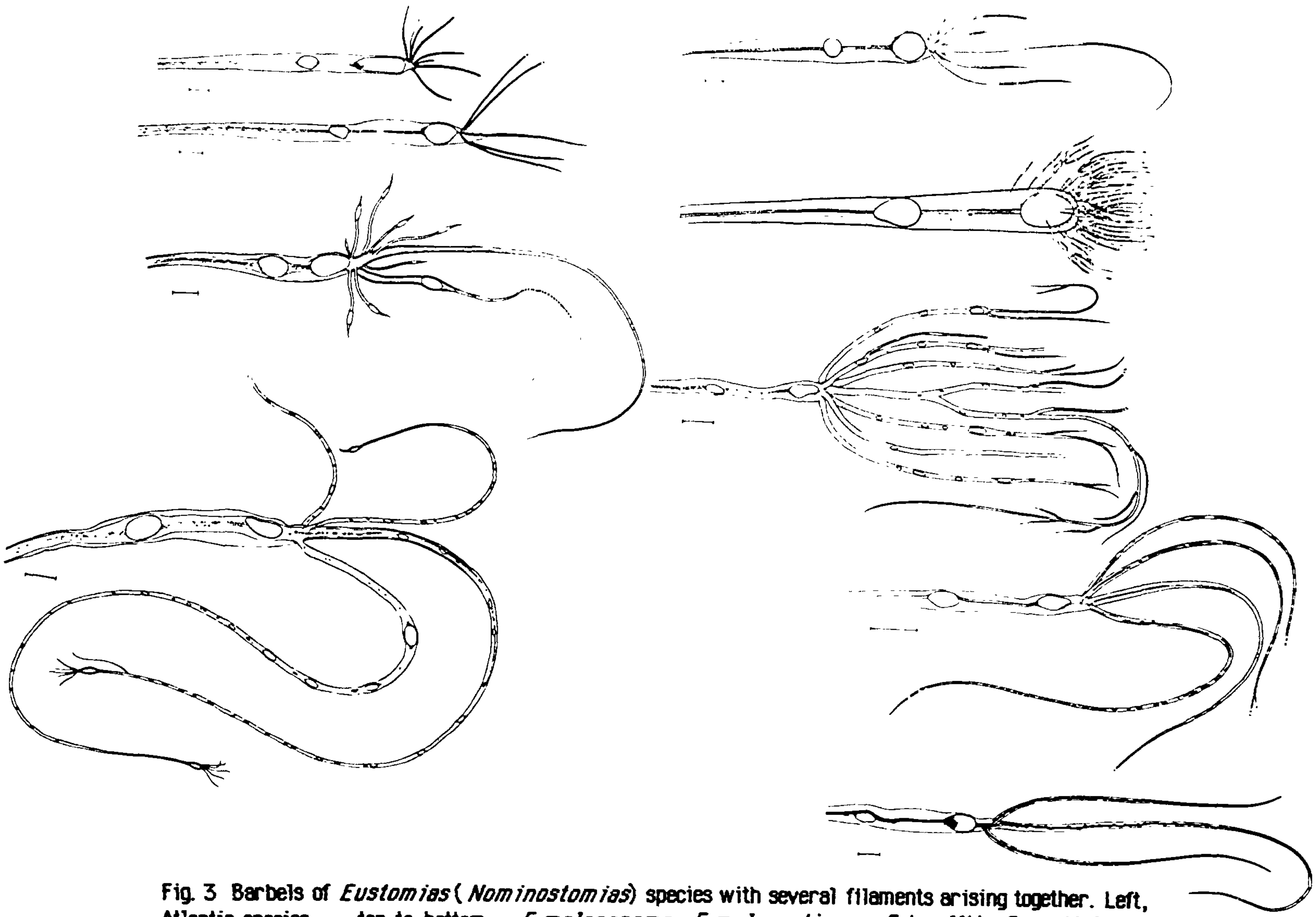

Fig. 3 Barbels of *Eustomias* (*Nominostomias*) species with several filaments arising together. Left, Atlantic species -- top to bottom: *E. melanonema, E. melanostigma, E. kreffti, E. posti.* Right, Indo-Pacific species -- top to bottom: *E. melanostigmoides, E. multifilis, E. medusa, E. bertelseni, E. suluensis.*

what I would have considered to be two species in 1964 are recognized today as being 24.

We were able to show that each of the well-represented forms differed from each other in relative growth and size of the barbel and/or one or more of its parts, including each of the bulbs, the distance between them, and the terminal filament. By inference, the poorly represented forms that showed such differences were also considered species. The fact that the Atlantic species turned out to have almost entirely separate geographic ranges (Fig. 4) reinforced the taxonomic decisions based on barbel morphology. Some, but not all the Pacific species appear to have separate ranges, (but the Pacific has not been sampled nearly as well as the Atlantic).

It should be noted that only one (*N. melanostigma*) of the 38 species in the subgenus *Nominostomias* occurs in both the Atlantic and the Indo-Pacific. In fact, of the approximately 110 species of *Eustomias* that we currently recognize, only 12 (including *N. melanostigma*) have not yet been shown to have slight, but consistent differences in the

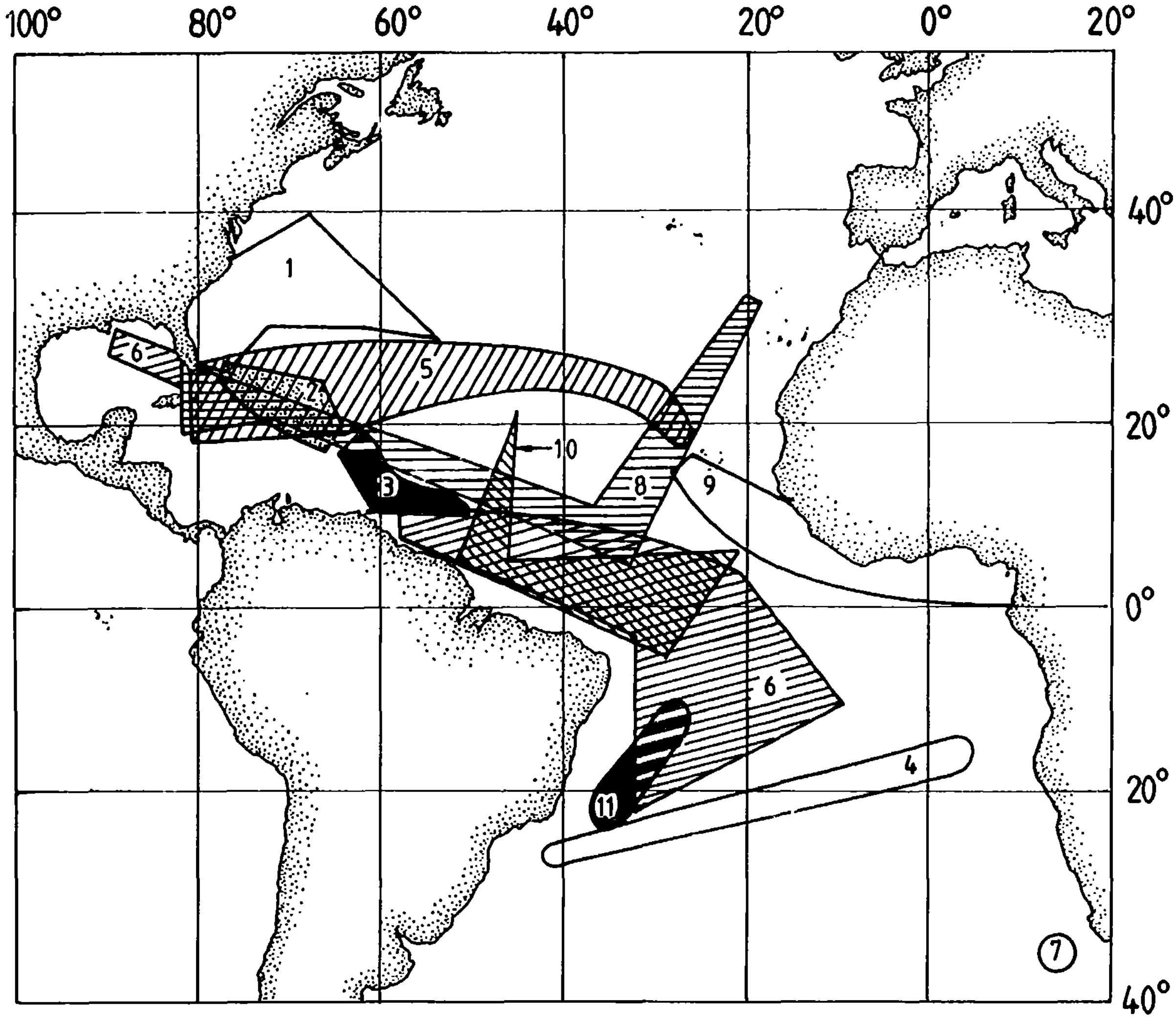

Fig. 4 Distributions of the 11 Atlantic species of *Eustomias*(*Nominostomias*). 1. *E. bibulbosus*; 2. *E. micraster*; 3. *E. bituberatus*; 4. *E. austratlanticus*; 5. *E. bimargaritatus*; 6. *E. arborifer*; 7. *E. grandibulbus*; 8. *E. melanostigma*; 9. *E. melanonema*; 10. *E. kreffti*; 11. *E. posti*. The only species with a range broadly overlapping that of other species is *E. arborifer* (6).

Atlantic and Indo-Pacific. We have not examined 11 of these species carefully, and I predict that inter-ocean differences will be found in all or most of them. Even within oceans, we are finding complexes of similar species where only one was recognized before. Circum-central tropical species would appear to be rare or non-existent. The only truly circumglobal oceanic species of *Eustomias* may be *E. trewavasae* which inhabits the southern Subtropical Convergence.

A taxonomic decision to call similar forms species is easier to accept, at least in practical terms, for allopatric forms than for syntopic forms. A case in point involves two Atlantic species, *Eustomias filifer* and *E. monodactylus* which I synonymized in 1964 and now consider valid again. They are obviously closely related, differing slightly but consistently in barbel structure (see Morrow & Gibbs, 1964), and both have been taken in the same areas in the Atlantic from 40°N to 40°S. Off Bermuda, the two have been taken in the same net haul, together with a third, undescribed species. This situation suggests the possibility of intraspecific polymorphism, but all three forms are distinct, and I prefer to call them species until evidence to the contrary is forthcoming.

The species concept expressed here is typological, based entirely on morphology. No genetic, biochemical, or physiological evidence is available. As far as I know, no live specimen of *Eustomias* has ever been taken, and no breeding or other experiments have been undertaken. The modus operandi is to take character variation into account as well as possible, and when morphological gaps remain, the distinct entities are considered species. If a gap involves only a single character, the decision should be the same. When the different morphologies are allopatric, such decisions are not too difficult to accept, but when they are syntopic, there will be more scepticism.

Whether or not this simple criterion is acceptable to others, it works, and I believe that the entities that it defines should be recognized formally and described as species. Unless a name is available, workers are unlikely to pay any attention to the entity in question or to look into the reasons or circumstances for the occurrence of such entities. I know that environmental factors can affect the phenotypic expression of characters. I know that polymorphism occurs. Until these things can be demonstrated, however, we should recognize discrete morphological entities as species. In doing so, I believe we will be right most of the time.

CONCLUSION

The genus *Eustomias* is not an isolated case. Most oceanic organisms are in need of discriminating taxonomic study. We should be suspicious of the many so-called species that have circumglobal or circum-central tropical distributions. In all probability they are complexes of subtly distinct species. Even species that have broad distributions within oceans should be suspect. We should take our clues from the restricted distribution patterns that more and more taxonomists are describing for their finely discriminated species. What one set of organisms displays can be expected and should be sought in others.

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THE GULF OF 'AQABA, A ZONE OF GREAT BIOLOGICAL INTEREST

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The Red Sea, a rather young sea, is connected to the Indian Ocean through the strait of Bab el Mandab at 12°40'N. It is entirely located in a very arid, hot and dry area. Owing to the increase in salinity, life conditions become harder in its two northern appendages, the shallow Gulf of Suez (depth < 60 m) and the deep Gulf of 'Aqaba. At the entrance of this Gulf, the narrow sill of Tiran (252m) rises between two >1200m deep trenches, with steep slopes.

Ecological conditions prevailing in the Gulf of 'Aqaba are known thanks to the Data Collecting Program in the Gulf of Elat ('Aqaba) (D.C.P.E.) initiated by the Heinz Steinitz Marine Biology Laboratory in 1974 (Reiss & Paperna, 1975; 1976; Shilo & Cohen, 1979; Shilo & Paperna, 1977). Surface temperature varies between 20°C in the winter and 27°C in the summer season; at about 150m temperature is 21°C. Salinity increases from the entrance owing to evaporation, reaching 40.8‰ and more in the depth (below 500m). There are no significant thermocline and halocline. Waters are oligotrophic but well oxygenated; the primary production is low.

Thaliacea, although collected at all depths, are mainly caught with closing nets in the upper layers, from 200m to the surface (>21°C). Doliolums and salps are only found, as pyrosomas were never recorded from the Red Sea. The thaliacean fauna is a mixture of Indo-Pacific and ubiquitous species (Table I). Although devoid of endemic species, this fauna exhibits original features.

1) Dwarfism shown by many species: e.g. the phorozoids and gonozooids of *Doliolum denticulatum* reach a length of 3-4mm (instead of 5mm and more in Atlantic specimens)(personal observation).

2) The remarkable presence of salp species rather uncommon in other seas (Godeaux, 1978; 1979; 1985). *Ritteriella amboinensis* is usually a rare species but it can be considered as characteristic of the Gulf, and *Brooksia rostrata* with a low catch frequency in the equatorial zone is rather abundant here. *Doliolina indicum*, an Indo-Pacific species, is regularly observed in the samples. On the contrary, *Salpa cylindrica*, the commonest species in the oceanic tropical waters, is found in the Red Sea proper but it is practically absent in the Gulf (a single catch). The same is true for *Salpa maxima (S. tuberculata)* often collected by the Manihine Expedition (1948-49) (Van Name, 1952) and now very rarely found. *Thalia rhomboides* is rare, except locally.

3) The occurrence of ecological races: Three species of Cladocera are known from the northern part of the Red Sea: *Evadne tergestina* (Gulf of 'Aqaba), *Evadne spinifera* (main basin) and *Penilia avirostris* (Gulf of Suez). The specimens of these three species are in external morphology strictly similar to the specimens from other parts of the world, as proved by the scanning microscope (Meurice, 1983; Meurice & Dauby, 1983). Probably, the differences are limited to the physiological level. As far as the Thaliacea are concerned, the same considerations may be evoked: e.g. the morphology of the specimens of *Thalia cicar* and *Doliolum denticulatum* are fully identical to those from both Atlantic and Indian Oceans.

Some species are truly tropical (*Thalia cicar, Ritteriella amboinensis*). Others, rather tolerant to temperature variations, (*Iasis zonaria, Brooksia rostrata*) became adapted to severe ecological conditions. Some species were not successful, as they occur only rarely, e.g. *Salpa cylindrica* and *Salpa maxima* while *Thalia democratica* and *Salpa fusiformis* are completely lacking.

Table I The thaliacean fauna of the Red Sea, Gulf of 'Aqaba, Gulf of Aden, and the Arabian Sea

Thaliacea	**Red Sea** **N**	 **S**	**Gulf of** **'Aqaba**	**Gulf of** **Aden**	**Arabian** **Sea**
Cyclosalpa pinn.sewelli				*	*
Cyclosalpa floridana	*				
_Cyclosalpa bakeri_*		*			
_Brooksia rostrata_*	*	*	*		
_Salpa maxima_*		*		*	
Salpa cylindrica	*	*	*	*	*
Ritteriella amboinensis	*	*	*	*	*
Ritteriella picteti			*		
Metcalfina hexagona				*	*
_Iasis zonaria_*	*	*	*	*	
_Thalia rhomboides_*	*	*	*	*	
Thalia cicar	*	*	*	*	*
Thalia orientalis				*	*
Pegea confoederata	*		*	*	
Doliolina muelleri					
Doliolina krohni	*	*	*		*
Doliolina intermedium		?			
Doliolina indicum	*	*	*	*	*
Doliolum denticulatum	*	*	*	*	*
Doliolum nationalis	*	*		*	*
Doliioletta gegenbauri tritonis		*	?	*	*
Pyrosoma spinosum				*	*
Pyrosoma agassizi			*		

(Compiled from different sources, Godeaux, 1985)

The fauna of the Red Sea is different from that of the Eastern Mediterranean; as a matter of fact there is no proof of former connections between the two seas. From the beginning, the fauna of the Red Sea was of Indo-Pacific origin but it is somewhat impoverished: e.g. *Thalia orientalis*, *Metcalfina hexagona* and the pyrosomas present in the Gulf of Aden and the surrounding areas are absent in the Red Sea. *Pegea confoederata* is present only in the southern part of the Red Sea.

Obviously, the fauna of the northern Red Sea, exemplified by the Thaliacea living in the Gulf of 'Aqaba, is the result of selective ecological pressures.

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SIZE SPECTRA IN MESOPELAGIC FISH ASSEMBLAGES*

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INTRODUCTION

The utility of allometric scaling of biological processes has long been obvious to physiologists (Calder, 1984), but application in ecology has only been appreciated rather recently (Peters, 1983). Size spectra have shown significant promise over taxonomically based approaches (Sheldon et al., 1977; Sprules & Holtby, 1979; Conover & Huntley, 1980), so much so that a SCOR working group has recommended this as an important research area (Matthews et al., 1984).

Studies of size spectra in the ocean emphasize the small particles that are readily measured using a Coulter Counter (Platt & Denman, 1978). Little work has been done involving pelagic organisms much larger than copepods. The biomass in different size classes is said to be approximately equal across the full spectrum, even though regional differences have been noted (Sheldon et al., 1972). Studies in lakes (Sprules & Knoechel, 1984) show a pattern which is quite "spikey", i.e. there is far more biomass in certain size classes than in others. The assumption continues to be that size spectra in oceanic assemblages are quite flat and that the biomass distribution is relatively uniform from class to class (Conover, 1979).

The purpose of the present study, part of a larger work on size structure in marine communities, is to compare size spectra based on the mesopelagic fish assemblages of faunal regions proposed for the Atlantic Ocean (Backus et al., 1977). Our concept is that pulses of production by the smaller size classes in a system propagate along the size spectrum as spikes of varying amplitude (see Silvert & Platt, 1980). By extension we argue that the more pronounced the pattern of seasonal primary production, the more "spikey" the spectrum will be. A second objective is to calculate the potential midwater fish production for the different areas using rules derived from considerations of allometric scaling.

METHODS

The data were derived from mesopelagic fish samples taken in over 1,000 Isaacs-Kidd midwater trawls made throughout the Atlantic Ocean from Iceland to the Southern Ocean (Backus & Craddock, 1977). Species lists were generated for each of 19 faunal regions, and the aggregate weight of each species was divided by the total number of specimens in each region to give the mean size for that species, expressed as log to the base two. Estimates of primary production for each faunal region were obtained by overlaying the regions on the primary production chart of Koblentz-Mischke et al. (1970) and integrating using a Hewlett-Packard digitiser.

Size spectra are usually expressed graphically as a frequency distribution, and are not easily quantified. To overcome this difficulty, the biomass spectrum is here expressed as a fractal (Mandelbrot, 1977), a measure useful for the analysis of complex structure (Bradbury et al., 1984; Morse et al., 1985). To calculate the fractal, the log of the distance along the curve of the spectrum is divided by the log of the distance along the abscissa over which the curve is plotted. No special ecological meaning should be attached to this use of a fractal; applied to size spectra it is an index only.

The fractal dimension of a spectrum is conceptually appealing. The dimension is independent of scale, i.e. the same fractal dimension is obtained whether one looks at a very small portion of a range or the entire range itself (Mark, 1984). This means that the fractal dimension of a spikey distribution will indicate spikeness whether a small portion (e.g. mesopelagic fishes) or the entire spectrum (e.g.

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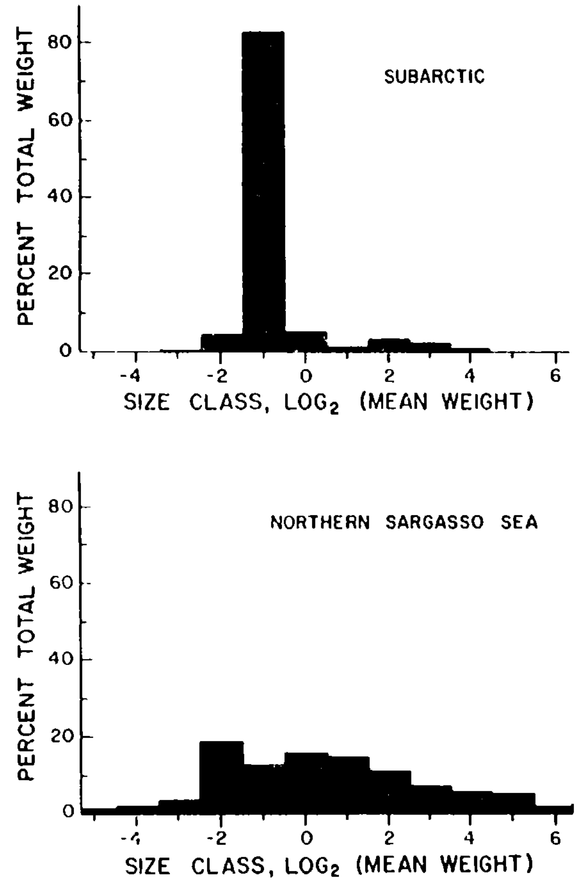

Fig. 1 Spikey and smooth biomass spectra based on oceanic mesopelagic fishes. Top: Atlantic Subarctic region, 53 stations (fractal dimension = 1.41). Bottom: Northern Sargasso Sea province in the fall, 47 stations (fractal dimension = 1.15).

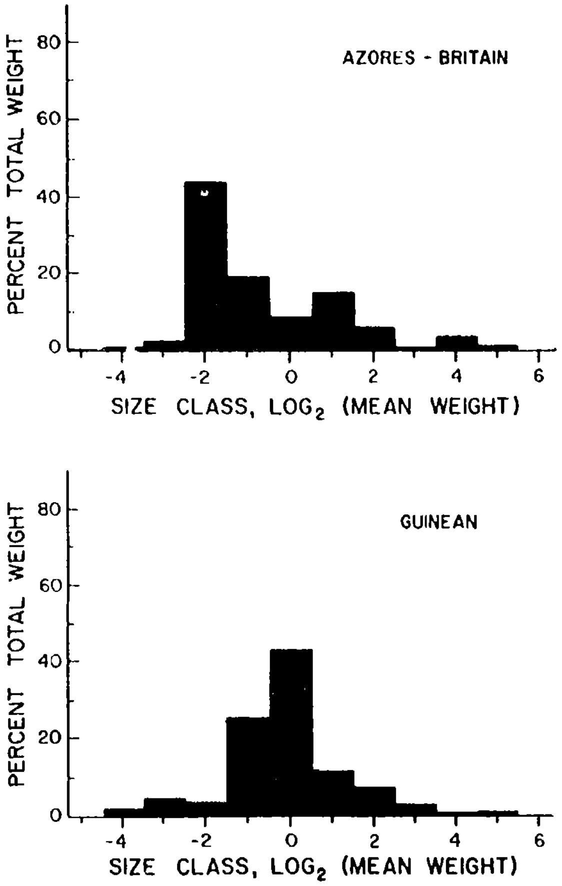

Fig. 2 Intermediate biomass spectra based on oceanic mesopelagic fishes. Top: Azores-Britain province, 105 stations (fractal dimension = 1.30). Bottom: Guinean province, 55 stations (fractal dimension = 1.26).

nannoplankton to whales) is examined. We have determined empirically that a purely spikey biomass spectrum (all biomass in one size class) will have a fractal dimension of two, and a purely smooth one (biomass the same in all size classes) will have a fractal dimension near one.

There is no allometric relationship that equates production directly to size, so the production:biomass (P/B) relationship was calculated instead. For fishes, this relationship is: $P/B = 0.44\ W^{-0.26}$ (Banse & Mosher, 1980). The equation is rearranged and separate calculations are made for each size class and summed to give relative annual production per station. Production is also expressed as an absolute value, gm fish/ha/yr, arrived at by dividing the calculated production figure by the total area swept by the trawl in each region.

RESULTS AND DISCUSSION

Biomass size spectra for mesopelagic fishes in the Atlantic range from the extremely spikey one characteristic of the Subarctic region to the very smooth one of the northern Sargasso Sea in fall (Fig. 1). The pattern follows that described for much smaller particles, with the flattest spectra occurring in the tropics and the most spikey towards the poles (Conover, 1979). As with the small particle spectra, areas intermediate in condition between the central gyre and the higher

Table I Faunal regions based on mesopelagic fish distributions in the Atlantic Ocean: number of stations (IKMT), estimated primary production (gm $C/m^2/yr$), fractal dimension, relative mesopelagic fish production based on the allometric relation, estimated absolute annual mesopelagic fish production (gm/ha/yr), and area ($10^5 km^2$).

Province	sta	prim prod	fractal dimension	rel prod	abs prod	area
Subarctic	53	426	1.41	230.6	71.1	45.9
Western Mediterranean	31	270	1.37	168.5	39.4	3.7
Guinean	55	189	1.26	62.7	17.9	77.4
Slope Water	54	278	1.36	85.5	16.1	4.9
Azores-Britain	105	200	1.30	40.8	14.4	29.8
Caribbean	52	210	1.29	69.6	12.7	18.8
N.North African	53	129	1.22	34.8	11.3	15.4
Amazon	73	215	1.28	39.2	9.9	42.0
S.North African	72	186	1.22	26.4	7.6	37.4
Northern Sargasso	86	77	1.32	27.6	7.2	32.8
Mediterranean Outflow	42	200	1.25	15.3	5.6	12.3
Eastern Mediterranean	35	200	1.34	35.4	5.6	11.7
Antillean	47	215	1.19	19.3	5.4	12.4
South Atlantic	94	70	1.24	12.0	5.2	101.6
Southern Sargasso	77	155	1.21	12.3	3.2	29.0

latitudes show intermediate spectra (Fig. 2). Thus, biomass spectra are not flat everywhere in the ocean; in fact, they are little different from the spectra shown for plankton in lakes (Sprules & Knoechel, 1984).

Based on the results of other studies (e.g. Bradbury & Reichelt, 1983), it was expected that the fractal dimensions of the biomass spectra would display either one or only a few discrete values. This situation would have been in keeping with the traditional characterisation of tropical, subtropical, temperate and polar oceans. This is not the case. There is a smooth range of fractal dimensions from 1.2 in the South Atlantic and southern Sargasso Sea to 1.4 for the Subarctic (Table I). In regard to the ecological relationships implied by the varying sizes of animals inhabitating them, the faunal regions grade rather uniformly from the central gyre condition to that of the highly seasonal northern ocean. The approach de-emphasizes clear distinctions between faunal regions, as does the recent faunal study of McKelvie (1985).

The fractal dimension can be used as a predictor of fish production, although the relationship is not linear (Fig. 3, Table I). Both this relationship and the regression for the linear semi-log relationship ($\log P = 9.08 F - 7.88$) are significant ($p<.01$). This result means, as is observed, that spikey biomass spectra characterise regions of high seasonal production. The fractal dimension offers an approach to the difficult problem of determining levels of production for an assemblage, and is particularly useful for comparative studies. It could also be used to predict production over the entire size spectrum in an area.

A fundamental concern is whether the production values based on the allometric relation have any basis in reality. This is difficult to test, because measurements of actual production have not been made. It is encouraging that measured values of primary production track those for fish production very well (Fig. 4, Table I). The chart of production based on size spectra (Fig. 5) resembles the familiar chart of primary

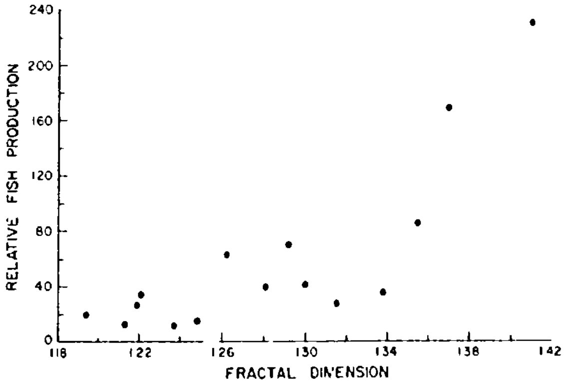

Fig. 3 Relative mesopelagic fish production based on the allometric relation $P/B=0.44W^{-0.26}$ as a function of fractal dimension for faunal provinces in the Atlantic; $r=0.80$, $p<.01$. Includes only regions with more than 30 station.

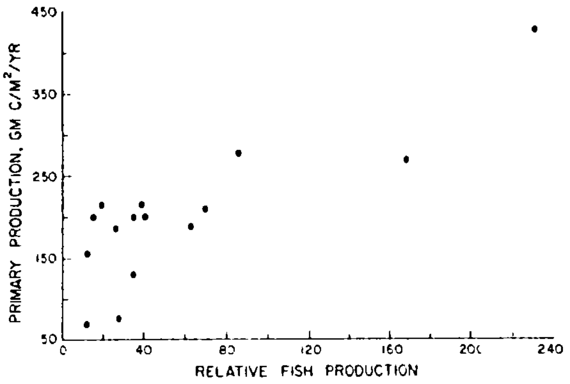

Fig. 4 Scatter plot of the relationship between relative mesopelagic fish production and primary production, gm $C/m^2/yr$; $r=0.83$, $p<.01$. Includes only regions with more than 30 stations.

production for the Atlantic. Lowest values are found in the central gyres, and the highest values are in high latitudes and special areas such as the Mauritanian upwelling.

The absolute values of mesopelagic fish production (Table I) are unrealistically low, with a total annual production of only about 50,000 tonnes predicted for the entire North Atlantic basin. But the calculations are based on the standing stock biomas as determined from the Woods Hole IKMT surveys, and independent estimates from the same regions suggest these data are low by at least two orders of magnitude (Gjosaeter & Kawaguchi, 1980). If the absolute production values are multiplied by 100, the new values seem much more in line. For example, the average annual catch of lanternfish in the South African purse seine fishery (9,450 tonnes) would then be about 9% of the annual mesopelagic fish production calculated here for the somewhat comparable Mauritanian Upwelling region, and about 12% of the production calculated for the Slope Water.

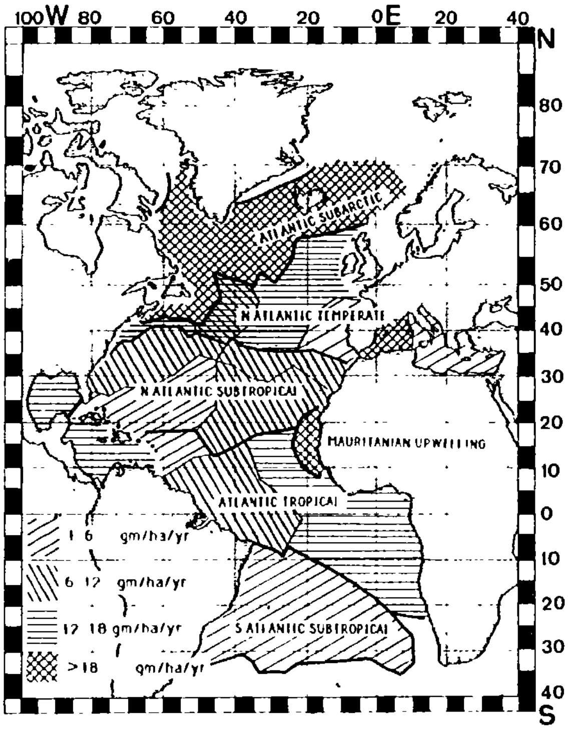

Fig. 5 Absolute mesopelagic fish production, based on the allometric relation of Banse & Mosher (1980), by faunal province in the Atlantic ocean. Data from table I; boundaries from Backus et al. (1977).

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TOWARD A STUDY OF THE BIOGEOGRAPHY OF PELAGIC CTENOPHORES

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INTRODUCTION

Ctenophores are one of the most difficult of all groups of pelagic animals to study. They are represented only sporadically in net collections, so that the majority of the large oceanographic expedition reports do not even mention them, and those few reports that do deal with them (Chun, 1898; 1900; Moser, 1903; 1909; Mortensen, 1912; 1913) report the collection of only a handful of specimens. One gains the impression, based on the results of these "quantitative" sampling studies, that ctenophores represent an insignificant fraction of the fauna of the open sea.

Over the past decade, however, collections made by SCUBA divers have revealed that only a small fraction of the epipelagic species can be collected with nets (Harbison et al., 1978). The reason for the discrepancy between the results of net collections and the results of SCUBA collections is obvious - most species of ctenophores are simply too delicate to be collected with convential plankton sampling techniques. Of those few species that can be collected with nets, only a small fraction can be preserved in recognizable condition. Therefore, most of the species commonly collected by SCUBA divers are never seen by most zooplankton ecologists. Six common epipelagic species are shown in figure 1. Many more could be shown, of course, such as the most ubiquitous of all of the epipelagic ctenophores, *Cestum veneris* Lesueur, 1813 (Harbison et al., 1978). It is obvious that the towed net is not the technique of choice in studying the biogeography of epipelagic ctenophores.

DISTRIBUTION PATTERNS

On a recent cruise (October to November 1984) in the Bahamas, where we used the submersible, the DSRV JOHNSON-SEA-LINK 11, to collect mesopelagic organisms, it soon became apparent that the epipelagic ctenophore fauna is extremely sparse, when compared with the midwater fauna (see Youngbluth, 1984a for a description of the collecting devices). We collected six species by SCUBA diving - *Ocyropsis maculata immaculata* Harbison & Miller (1986); *Eurhamphaea vexilligera* Gegenbaur, 1856; *Bolinopsis vitrea* Agassiz, 1860; *Hormiphora* sp.; *Cestum veneris;* and *Beroe* sp. At depths of about 600m, however, we collected at least 22 different species of ctenophores, of which only five have been previously described. (Figs 1e, 2). Of these five species, only two, *Bathocyroe fosteri* Madin & Harbison, 1978a and *Bathyctena chuni* (Moser, 1909) had been described as deep-sea species. Two of the others, *Kiyohimea aurita* Komai & Tokioka, 1940 and *Thalassocalyce inconstans* Madin & Harbison, 1978b, are occasionally advected into surface waters. The last species, *Euramphaea vexilligera,* appears to be a truly epipelagic animal, since we collected only a single specimen with the submersible, while numerous specimens were collected with SCUBA. Since over 75% of the species of ctenophores that we collected with the submersible were undescribed, and there were three times as many species at 600m than in the upper 30m, the most reasonable conclusion that can be drawn is that the vast majority of ctenophores live in the deep sea, and that they are undescribed.

In a recent paper (Harbison, 1985), I suggested that ctenophores evolved in the open ocean , since all but one specialized order are pelagic, and ctenophores are found in their greatest diversity in the open sea. I would like to modify this speculation even farther, and suggest that it appears likely that most of the evolution within the group has taken place in the deep ocean.

Ctenophores appear to be extremely well-adapted to live there. Their large food-collecting apparatuses, their ability to "degrow" when starved, and their delicacy strongly suggest that they have evolved in an environment free from hard surfaces, turbulence, mechanical stresses, and low in food. Almost all species of ctenophores are strongly bioluminescent, a character shared with many other mesopelagic groups. If ctenophores did indeed evolve in the deep ocean, then we are faced with a paradoxical situation that reveals how little we really know about life in this region of the ocean - this group of predominately midwater animals is known almost entirely from collections made close to shore or in the epipelagic!

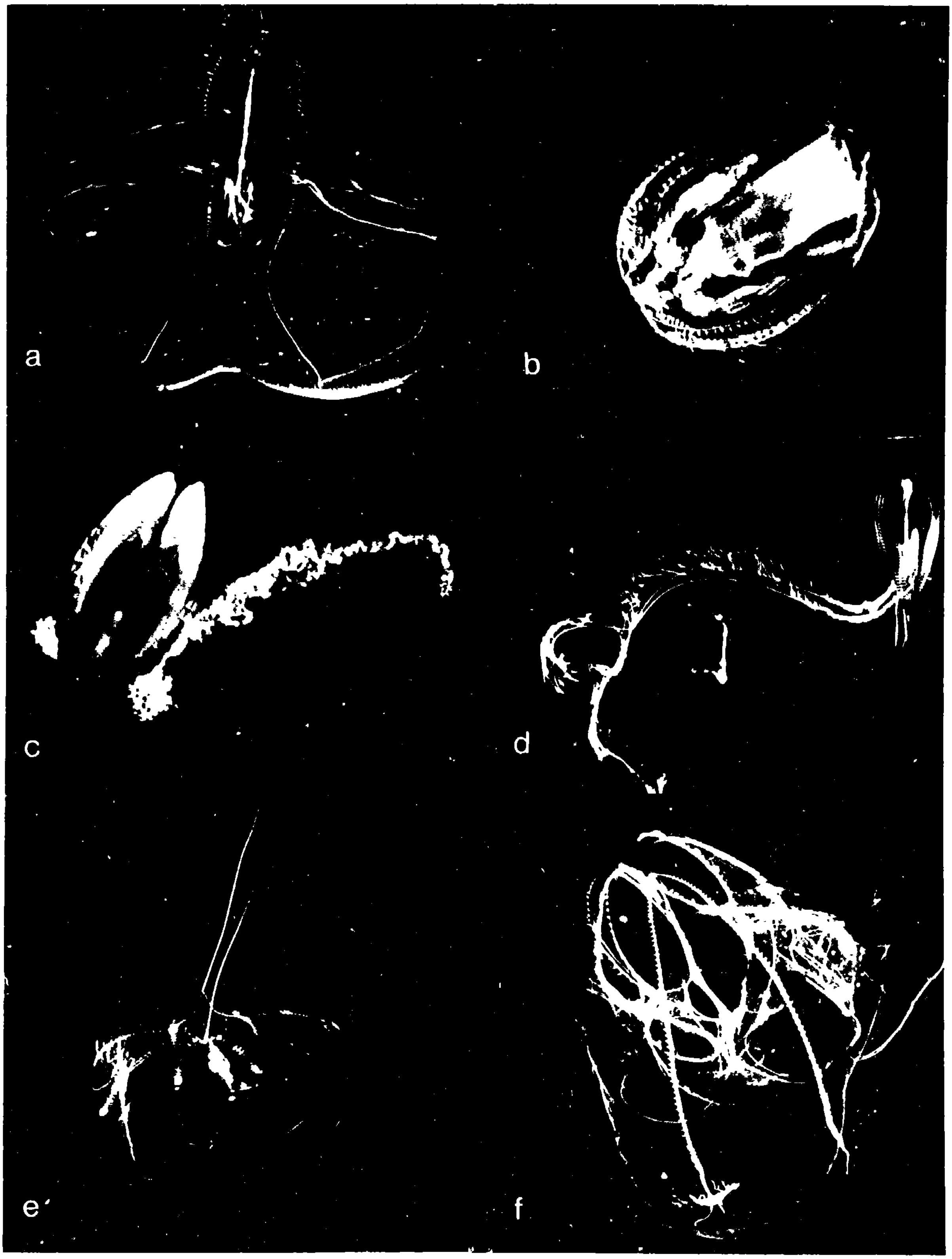
I did not expect to be confronted with such a great number of undescribed ctenophores, and P.R.Pugh (Institute of Oceanographic Sciences), who studied the siphonophores we collected with the submersible, had results similar to mine. He found that of the thirty species of siphonophores we collected, fifteen are probably undescribed. Most of these undescribed species were physonects, and one of them was over ten meters long! That such a great number of previously unknown large animals could be collected in only three weeks of diving with a submersible in a small area in the Bahamas indicates, I think, that the study of these diverse, and potentially important groups of mesopelagic organisms is only beginning.

In terrestrial biogeography, it is well-known that the distribution of many organisms is dependent on both physical and biotic factors. However, in pelagic biogeography, most workers concentrate on the physical factors, giving only slight attention to the potential importance of biotic factors in determining distribution patterns. For example, in terrestrial biogeography, the importance of plant hosts in determining the distribution of insects is well-known, yet in pelagic biogeography only a few analogous examples can be cited. I think that this does not imply that biotic factors are of little consequence in the pelagic environment, but merely reflects our present ignorance. Figure 1f shows a pelagic relationship analogous to that between insects and plants. The hyperiid amphipod, *Glossocephalus milne-edwards*, Bovallius,1887, is a highly specific parasite on species of the ctenophore, *Bolinopsis*. Many other hyperiid amphipods are also found in association with large gelatinous organisms, and often these associations are obligate (Harbison et al., 1977). Since biological oceanographers were unaware of these relationships (see Shulenberger, 1979 as an example), they attempted to correlate the distribution patterns of hyperiid amphipods only with water masses or other chemical-physical parameters, rather than with the presence of their gelatinous hosts (see Laval, 1980 for a discussion of this).

CONCLUSIONS

It is becoming more and more apparent, as we learn more about the behaviour and physiology of oceanic organisms, that very few animals are planktonic in the classical sense (that is, simply passive drifters), and it is also becoming apparent that biotic factors are probably as important in determining distribution patterns of pelagic organisms as they are in determining the distribution patterns of terrestrial organisms.

Fig. 1 Widely distributed epipelagic ctenophores, rarely if ever reported from net sampling studies. (a) The lobate, *Leucothea multicornis* (Quoy & Gaimard, 1824), photographed in situ in the western North Atlantic (0.5x). (b) *Haeckelia rubra* (Gegenbauer et al., 1853), a small cydippid whose tentacles lack tentilla (11x). (c) The tiny blue cydippid, *Tinerfe cyanea* (Chun, 1889), was described from the Canaries, but this specimen was collected in the Coral Sea off Australia (16x). (d) The cydippid, *Callianira bialata* Chiaje, 1848, is usually collected by SCUBA divers at night, and thus may be a vertical migrator (1.2x). (e) The lobate, *Eurhamphaea vexilligera*, is common in oligotrophic regions of the tropical and subtropical Atlantic and Pacific. Photographed in situ in the Coral Sea (0.5x). (f) The lobate, *Bolinopsis vitrea*, is often found near coral reefs in both the Atlantic and Pacific. An hyperiid amphipod, *Glossocephalus milne-edwardsi*, can be seen on the oral lobe of this animal (0.8x).



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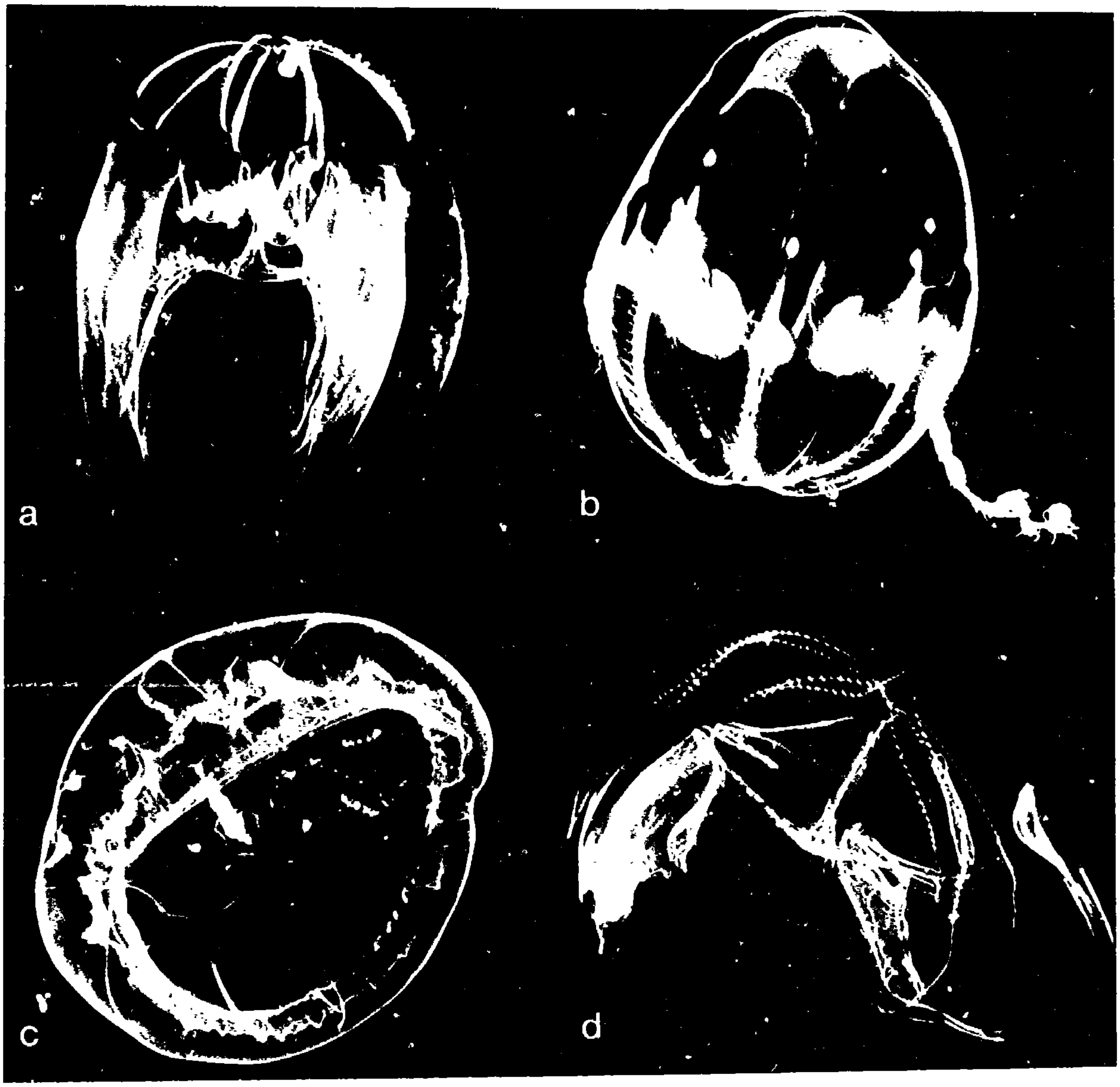

Fig. 2 Four mesopelagic ctenophores, all collected in the fall of 1984 in the Bahamas with a submersible. (a) The lobate, *Bathocyroe fosteri*, has been collected below 400m. in both the Atlantic and Pacific, and may be the most abundant of all presently known ctenophores (1.5x). (b) The cydippid, *Bathyctena chuni*, was previously known from the Indian Ocean and eastern Atlantic (4.5x). (c) *Thalassocalyce inconstans* was thought to be a rare epipelagic species, but submersible collections have revealed that it is common at depths below 400m. (1x). (d) The lobate, *Kiyohimea aurita*, is often found at mesopelagic depths (0.4x). See Youngbluth (1984b) for other submersible records from the Bahamas.

Progress in pelagic biogeography will only come through an improved understanding of all the factors responsible for the distribution and abundance of pelagic organisms. Increased efforts must be made to collect organisms such as ctenophores, and to concentrate more on the observation of midwater organisms in the field. At present, very few submersibles are available that are adequate for the study or collection of animals in midwater. Elucidation of the distribution patterns of large gelatinous organisms and of the animals that depend on them for some part of their life histories will only be achieved by improving our ability to study them in situ. We need to develop techniques to quantify these "uncollectable" organisms, and we need to be able to spend more time in the field.

The development of an undersea research vessel, large enough to carry submersibles and support a scientific team of about ten people, would greatly accelerate progress (Harbison, 1982). With such a research vessel, we could spend extended periods at depth, comparing visual counts with submersible and net collections. We could also develop techniques for the study of midwater animals similar to those used by terrestrial ecologists and biogeographers. Until we are able to do this, pelagic biogeography will continue to lag far behind terrestrial and nearshore biogeography.

ACKNOWLEDGMENTS

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PROBLEMS IN OPEN-OCEAN PHYTOPLANKTON BIOGEOGRAPHY

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INTRODUCTION

The phytoplankton consists of single-celled primary producers mostly belonging to the smallest size-fraction of the marine plankton (0.2 - 2000µm). Asexual, vegetative reproduction predominates in all taxonomic groups, and the reproduction rate is high, 0.2 - 2 divisions per day or more. These characteristics place the phytoplankton in a unique position compared to other inhabitants of the open ocean. The small size qualifies the phytoplankton as passive drifters in a vast environment although as primary producers, restricted to the euphotic zone. The predominance of vegetative reproduction and probably also the short reproduction time enable the species not only to survive but also to reproduce outside their "range bases" as defined by Semina (1979). The overwhelming dominance of the smaller individuals of the nanoplanktonic diatom *Nitzschia pseudonana* in the open waters of the Norwegian Sea and the Subantarctic illustrates the ability to survive by vegetative formation with a gradual diminution of the cell size; an ability which may be responsible for the global distribution of this species (Hasle, 1976). Although the characteristics mentioned probably influence the latitudinal range of phytoplankton species, they may have consequences for the longitudinal distribution as well, i.e. coastal species may drift into oceanic waters and continue to divide and vice versa.

CHARACTERIZATION OF OCEANIC ASSEMBLAGES

By the successful culturing of planktonic algae isolated from the open ocean physiological and ecological attributes of the oceanic phytoplankton have now been investigated. Algae with primarily oceanic distribution were shown to be particularly efficient in utilizing the small nitrogen concentrations of the oceanic waters (Eppley et al., 1969), and furthermore to have generally lower requirements for zinc and iron than species living in coastal waters with much higher concentrations of these micro-nutrients (Brand et al., 1983).

Study of phytoplankton collected in the open waters of the Norwegian Sea, the Subantarctic and the Pacific Ocean by water bottles, preserved in neutralized formaldehyde and examined in the inverted microscope (Halldal, 1953; Hasle, 1969; Fryxell et al., 1979) has indicated further characteristics of oceanic assemblages: firstly high cell numbers of small unidentified flagellates, secondly a coccolithophorid flora rich in species and often numerically predominant, and finally a dinoflagellate flora rich in species but not particularly abundant. Moreover, recent research has shown that the picoplankton (0.2 - 2µm), including blue-green algae, forms a significant component of the open-ocean ecosystem (Platt et al., 1983).

The most abundant coccolithophorid in the investigation from the central Pacific by Fryxell et al. (1979) was *Emiliania huxleyi* (by Fryxell et al., recorded under the synonym *Gephyrocapsa huxleyi*). Oceanic clones of this species were used by Eppley et al. (1969) as representative of oceanic plankton to test physiological and ecological attributes with the result mentioned above. However, *E. huxleyi* occurs regularly in mass concentrations in Norwegian fjords during summer. The diatoms *Nitzschia closterium* and *N. bicapitata* and the dinoflagellate *Oxytoxum variabile* also belonged to the ten most abundant taxa in the investigation by Fryxell et al., (1979); the former is most probably an ubiquist while the other two appear to be true oceanic species. Another, extensively studied, oceanic species is *Thalassiosira oceanica* , a diatom distinct from the allied neritic *Thalassiosira pseudonana* by ecological and physiological properties as well as morphological characters (Brand et al., 1983; Hasle, 1983), but, in the past regarded as belonging to *T. pseudonana* as a suggested oceanic "race".

BIOGEOGRAPHY OF THE OPEN OCEAN

The classification of the planktonic algae as neritic (including inshore and coastal), oceanic and panthalassic (present in neritic and oceanic waters) necessarily depends on the extent of the information available on the frequency of occurrence in particular areas. It is also very much dependent on accurate identifications of taxa and on the personal opinions of planktologists. For instance, many of the species classified as oceanic by Gran (1912) occur regularly in the Oslofjord and are thus unacceptable to the present author as "oceanic".

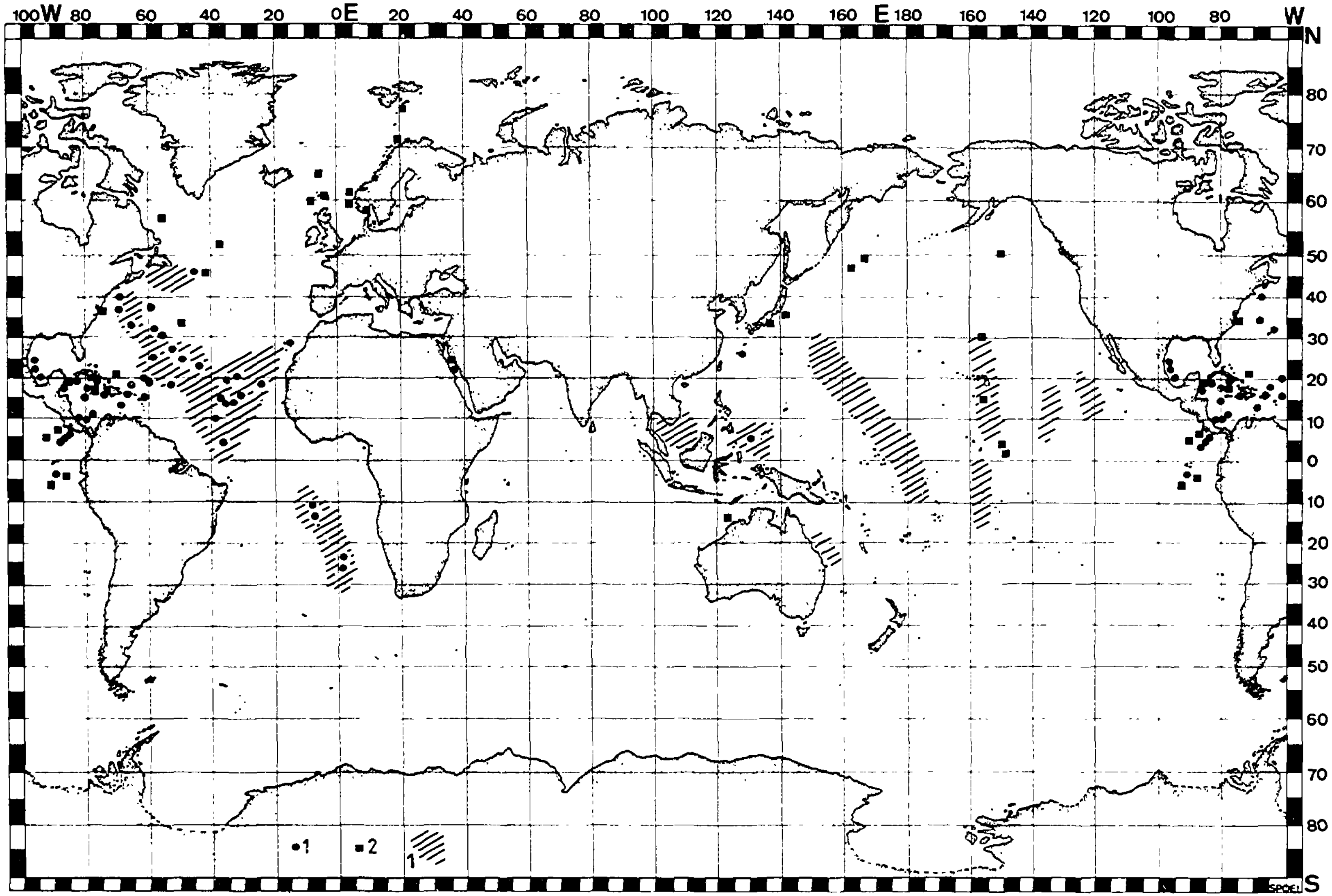
However, a review of more modern pertinent literature tends to add to the confusion rather than to reveal a possible pattern differentiating between coastal and oceanic species. For instance, *Umbellosphaera irregularis* shows the more common coccolithophorid distribution, being better represented in the open ocean than in coastal areas and restricted by temperature boundaries (McIntyre & Bé, 1967), while the few coccolithophorids present in colder waters of the open ocean occur inshore as well (e.g. *Emiliania huxleyi, Calciopappus caudatus*). Moreover, Hallegraeff (1984) in an investigation of 42 coccolithophorid species in Australian waters, recorded three species from oceanic and three from coastal stations while the rest were present in both habitats.

Ceratium is an autotrophic, widely distributed dinoflagellate genus with the highest species diversity in the warmer seas. A study of 58 species recorded from the Pacific and the North Atlantic Oceans revealed a predominance of oceanic and panthalassic species (Graham & Bronikovsky, 1944). Seven species were recorded north of 60°N whereas most of the remaining species were recorded only south of 40°N. The species with the widest latitudinal distribution were abundant in coastal waters and scarce, if recorded at all, in the open ocean (e.g. *C. furca*). The tropical species, on the other hand, were abundant in the open ocean and absent from the coastal stations (e.g. *C. euarcuatum*). *Ceratium arcticum* is one of the few species of the genus characteristic of cold waters. As recorded by Graham & Bronikovsky (1944), it appears to be oceanic.

The diatoms *Nitzschia bicapitata, Roperia tesselata* and *Nitzschia americana* occcur in temperate and tropical zones, *N. bicapitata* being recorded betweeen 66°N and 62°S, *R. tesselata* between 66°N and 57°S, and *N. americana* between 54°N and 44°S (Hasle, 1976). *Nitzschia americana* is a coastal species whereas the two others have not been recorded inshore (e.g. in Norwegian fjords) and may well be regarded as oceanic species often drifted into coastal waters, *R. tesselata* more so than *N. bicapitata*. The diatoms *Thalassiosira poroseriata* and *Nitzschia* (*Fragilariopsis*) *kerguelensis* may also be classified as oceanic, though cold water, species. The former has been recorded between 80°N and 49°N in the North Atlantic Ocean and between ca. 76°S and 40°S in the Southern Ocean and fairly close to the coasts of South America. *Nitschia kerguelensis* is widely distributed in the Subantarctic and partly also in the Antarctic Zone and in addition has been found "to be scarce but nearly always present" from 40°S to 30°N in the Atlantic Ocean (Van der Spoel et al., 1973 : 540).

DISCUSSION

This paper was started with the intention to give a characterization of the open-ocean phytoplankton in order to reveal possible unique features. To do so, it seemed necessary to use species which in their distribution could be classified as oceanic and to compare them with taxonomically related coastal and inshore species. The study showed, however, that the number of exclusively oceanic species present in the open ocean is surprisingly low compared to the number of panthalassic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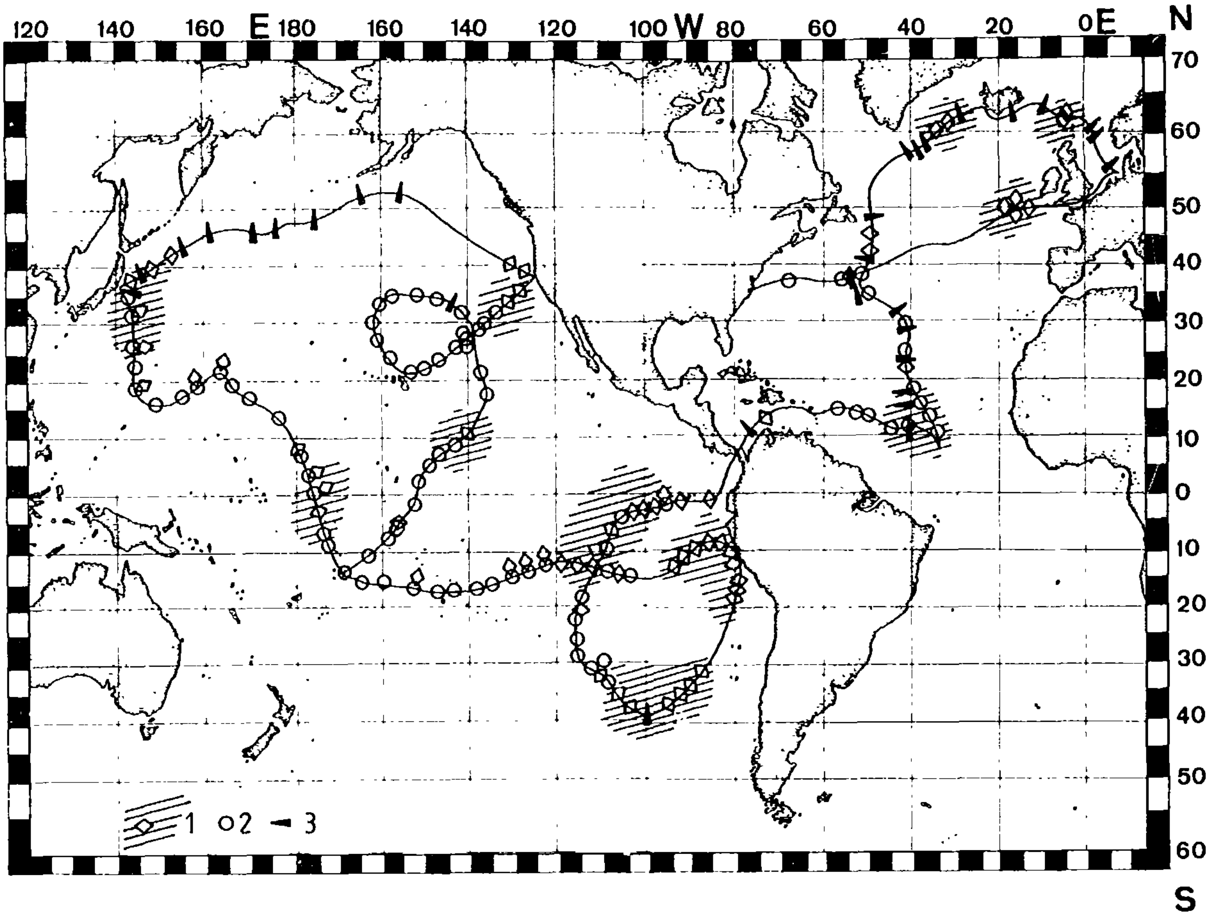

Fig. 2 The distribution of the panthalassic, cosmopolitan (?) dinoflagellate *Ceratium furca* (1), the oceanic, tropical dinoflagellate *Ceratium euarcuatum* (2), and the oceanic, cold-water dinoflagellate *Ceratium arcticum* (3).

phytoplankton species. In other words, a panthalassic species may have the properties necessary for life in the open ocean.

The open ocean, with no land barriers and the comparatively stable chemical and physical parameters, offers the ideal possibility for wide distribution ranges of the mainly passively drifting phytoplankton species. Moreover, to be panthalassic a species has to be tolerant of environmental fluctuations and could therefore in general be expected to have a wider biogeographical range latitudinally than an oceanic species. Inside the oceanic biogeographic zones, however, the oceanic as well as the panthalassic species would be expected to be more widely distributed than would the species present in the coastal zones.

The coccolithophorid *Emiliania huxleyi* and probably also *Calciopappus caudatus* may serve as examples of phytoplankton species present in the open ocean tolerant enough to survive in coastal waters and in various biogeographical zones, thus being panthalassic and cosmopolitan although *C. caudatus* has so far been recorded only at lower latitudes of the southern hemisphere (Fig. 1)(McIntyre & Bé, 1967: Fig. 8). The dinoflagellate *Ceratium furca* (Fig. 2) and the diatom *Nitzschia*

Fig. 1 The distribution of the oceanic, tropical-subtropical coccolithophorid *Umbellosphaera irregularis* (1) and the panthalassic, cosmopolitan (?) coccolithophorid *Calciopappus caudatus* (2).

pseudonana (Hasle, 1976: Fig. 37) have a distribution pattern similar to that of the two coccolithophorids although *C. furca* is probably more abundant in the open ocean and *N. pseudonana* may well be classified as oceanic. The records of the coccolithophorid *Umbellosphaera irregularis* (Fig. 1), the dinoflagellate *Ceratium euarcuatum* (Fig. 2) and the diatoms *Nitzschia bicapitata* and *Roperia tessalata* (Fig. 3) signify an oceanic distribution pattern. But, whereas the coccolithophorid and the *Ceratium* species are restricted to the tropical-subtropical zone as is usual for these groups, the two diatoms have such a wide latitudinal distribution that it may be questioned whether they are tropical or cosmopolitan. *Ceratium arcticum* and the diatoms *Thalassiosira poroseriata* and *Nitzschia kerguelensis* as cold-water oceanic species exhibit three different biogeographic patterns. *Ceratium arcticum* is restricted to the northern hemisphere (Fig. 2 which includes var. *longipes,* see Graham & Bronikovsky, 1944). *Thalassiosira poroseriata* has been recorded from both hemispheres but not from the tropical- subtropical zone (Fig. 4). *Nitzschia kerguelensis* has its main distribution area in the Southern Ocean, and its presence as far as north as 30°N illustrates the ability of an oceanic/panthalassic species to survive outside the basis of its species range (Fig. 4). Finally, the distribution of the three tropical-subtropical or cosmopolitan diatoms illustrates the more limited range of a coastal than of oceanic/panthalassic species (Fig. 3).

CONCLUDING REMARKS

These examples demonstrate a highly complex mosaic of biogeographical patterns, and a not very distinct trend for species present in the open ocean to have wider latitudinal ranges than coastal species. Except for this, no really unique features of the open-ocean phytoplankton biogeography are discernible. This may be true: the open ocean phytoplankton distributions may be much more complex than those of the coastal waters. Another reason for the lack of more definitive results is a lack of relevant data. It is therefore desirable that a greater interest in this underdeveloped field of biogeography can be stimulated in the near future.

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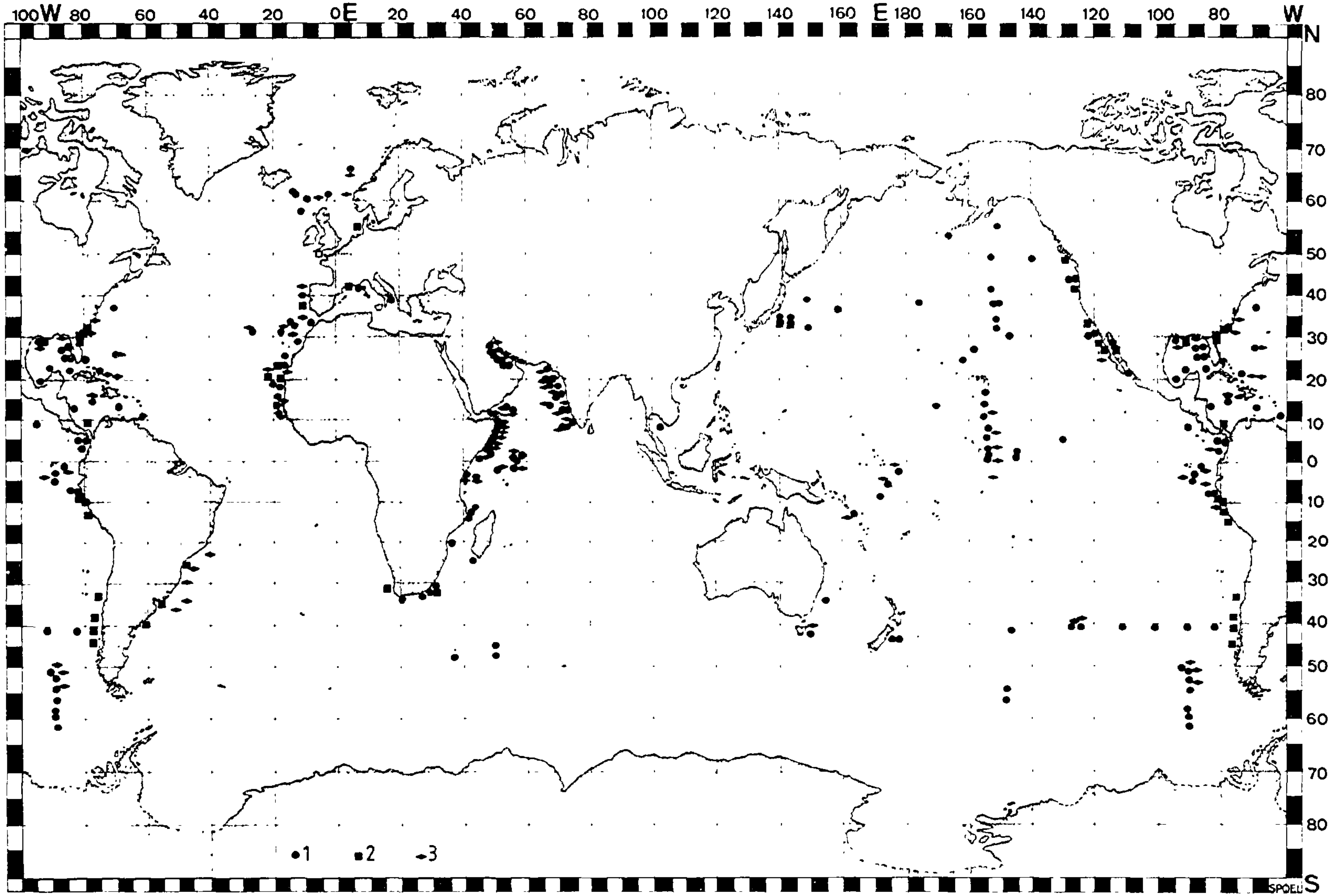
Fig. 3 The distribution of the oceanic, tropical-subtropical or cosmopolitan diatoms *Nitzschia bicapitata* (1) and *Roperia tesselata* (3), and the coastal, tropical-subtropical or cosmopolitan diatom *Nitzschia americana*(2).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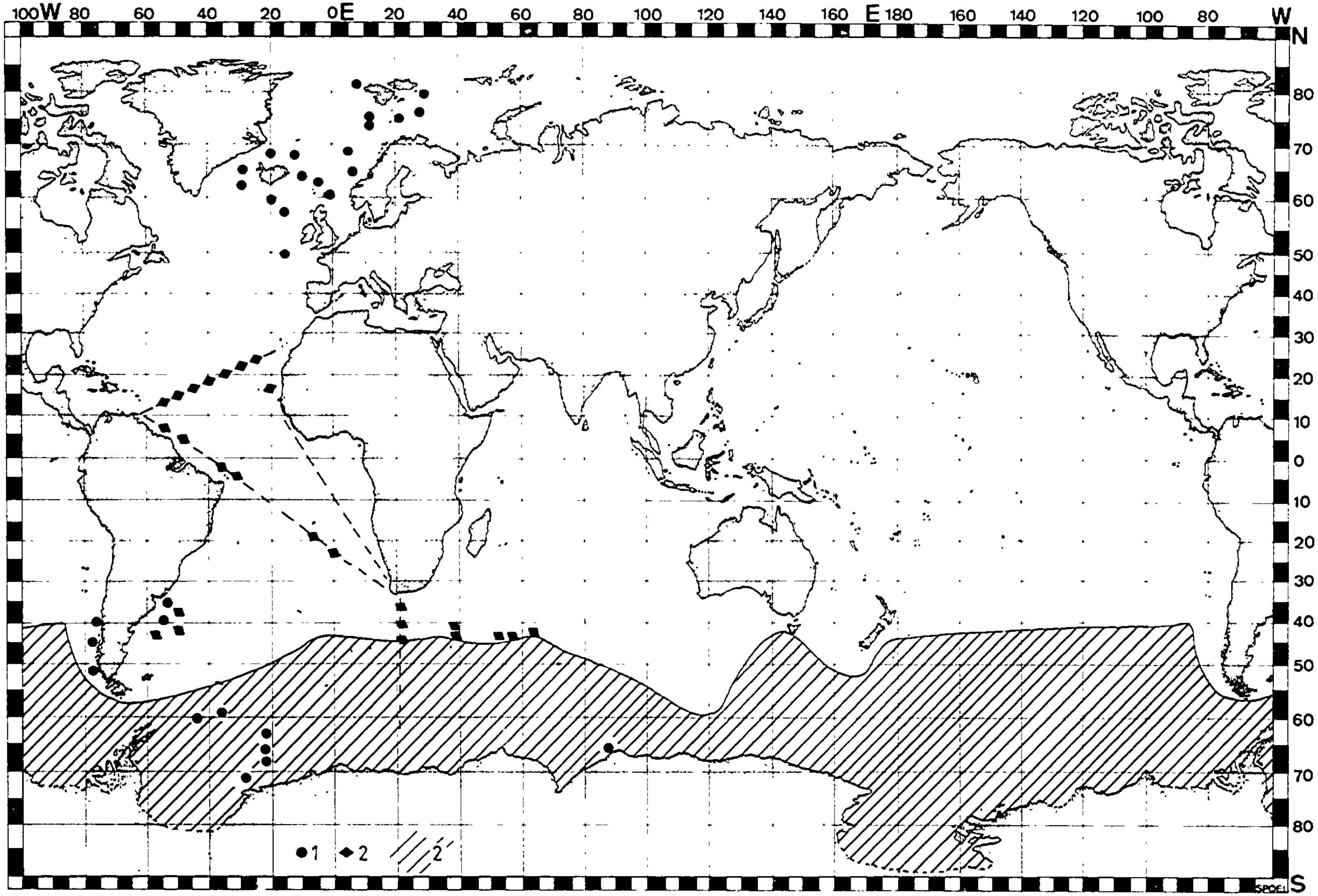
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Fig. 4 The distribution of the oceanic, cold-water diatoms *Thalassiosira poroseriata* (1) and *Nitzschia kerguelensis*(2).

PATCHES, NICHES, AND OCEANIC BIOGEOGRAPHY

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INTRODUCTION

After early emphasis on taxonomy and ocean-wide biogeography, the interests of most plankton ecologists turned towards sampling smaller and smaller spatial dimensions until today much work deals with the micro-scale (centimeters to meters). This focus on small scales has evolved, in part, in an effort to understand such things as competition, resource utilization, and the "paradox of the plankton". As a result, the study of the spatial limits and temporal variations of plankton distributions has been neglected, even though these features are not well understood. The recent research, however, is of biogeographic value in that it has given us a reasonably clear picture of distributional variability (i.e. patchiness) of many species over scales from meters to 1000's of kilometers. This information can provide a basis for ideas about the possible mechanics controlling species limits and the design of field sampling needed to test hypothesis arising from these ideas.

HORIZONTAL DISTRIBUTIONS

One of the features of patchiness that is evident from a synthesis of these studies is the hierarchical nature of the variability (Haury et al., 1978; Mackas et al., 1985). This results in distributions at the smallest scales appearing almost exactly like those measured over 100's to 1000's of kilometers. To illustrate this point, figure 1 replots onto comparable scales a few of the data collected over the past 25 years. The data selection emphasizes that, for many species over most of their ranges, there are very few or no "holes" (zeroes) in their distributions. These and much other data suggest that most heterogeneity in the plankton can best be described by frequency distribution models such as Cassie's (1963) varying mean hypothesis; patches with discrete boundaries (swarms) are rare.

Figure 1 does not present details of community aspects of such distributions; recent work,

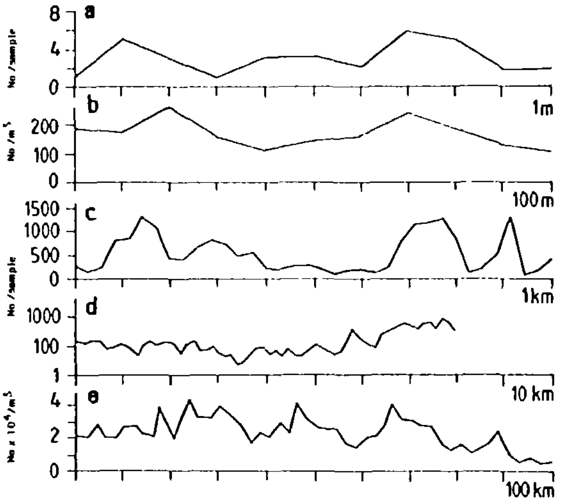

Fig. 1 Horizontal distribution of various zooplankton species at scales ranging from one meter to 100 kilometers plotted to emphasize the similarity between profiles regardless of scale of sampling and the apparent lack of "holes" (zeroes) in distributions. No adequate data were found to illustrate the 10m scale; the 1000km scale can be represented by the data of Barraclough et al. (1969) for layers of *Calanus cristatus* but are not shown because of difficulty in plotting. Data sources and ancillary information: a) Cassie (1959), *Polydora* larvae, pump samples from 50cm; b) Haury et al. (1983), *Calanus finmarchicus* copepodites, Longhurst-Hardy Plankton recorder samples from 15m; c) Smith et al. (1976), *Acartia clausi* males, pump samples from 7m; d) Cassie (1960), *Paracalanus parvus*, pump samples from 5m ; e) Mackas (1977), mixed species, pump samples from 3m passed through electronic counter. A considerable number of other sources describing distributions of other species at other depths using different collection techniques could have been used to illustrate the same points.

however, has shown that much of the patchiness is multispecies in character (e.g. Haury & Wiebe, 1982), or at least made up of homogeneous faunal assemblages (e.g. Star & Mullin, 1981; Mullin & Williams, 1983). Where a particular species may be absent in a transect probably depends more in interactions of its vertical distribution and rarity with sampling technique (e.g. Haury et al., 1983; Wiebe & Holland, 1968; McGowan & Fraundorf, 1966) than from any extended region of zero abundance. This continuity of distribution, coupled with the potential for the ambits of individual organisms to be large enough to bring species together in the same volume to interact, means that over a wide range of scales members of many species are not isolated from competitors, predators, and each other. Thus their environment may be fairly predictable over their lifetimes from the standpoint of community structure. This generalization may hold for much of the open ocean, but perhaps not for places like the California Current, which is an ecotone (McGowan, 1974; 1977).

VERTICAL DISTRIBUTIONS

The above considerations can be extended to vertical distributions as well; several studies (e.g. Boxshall, 1977; McGowan & Walker, 1979) have provided evidence that species do not divide the water column into a multiplicity of niches, defined in the simplest way as separation by depth. This lack of vertical separation can be illustrated in two ways:

1) distributions of species reveal that many have a similar characteristic pattern, i.e. note there are only a few generalized patterns for many species (Fig. 2);

2) individual species of a group having a similar pattern greatly overlap in their distributions (Fig. 3).

When vertical distributions are sampled with greater resolution, considerable overlap is still evident, indicating the absence of vertical niche separation (Fig. 4). Vertical mobility, especially diel vertical migrations, coupled with vertical variations in horizontal current structure, would be expected to have an even more important integrating effect on potential species interactions than the horizontal component of ambits.

BIOGEOGRAPHIC IMPLICATIONS

The motivation for much of the recent work on small-scale distributions of zooplankton is the hope that by looking at distributions on spatial

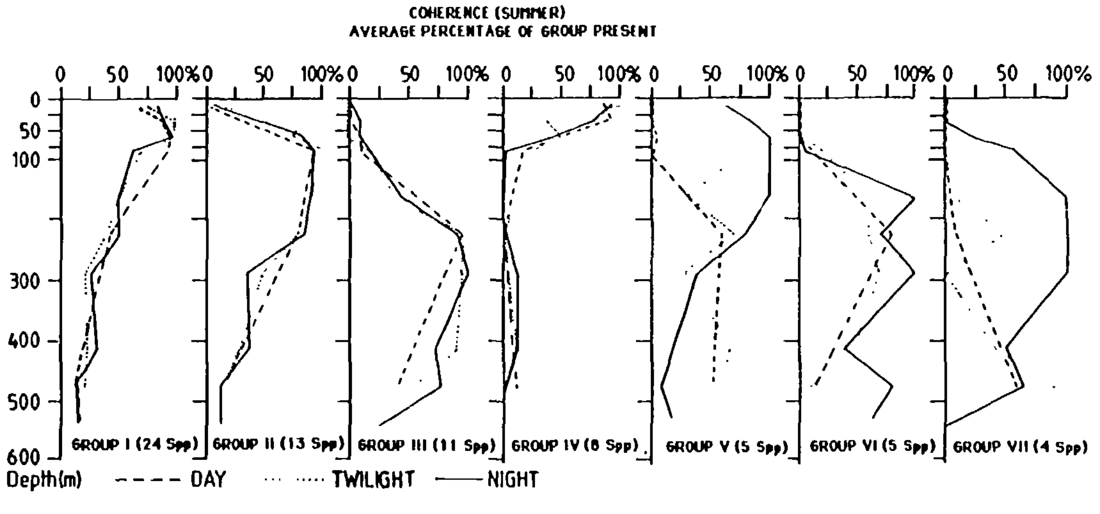

Fig. 2 Example of the extensive overlap in vertical distributions of copepods of the North Pacific central gyre. A total of 70 species grouped into 7 patterns, two-thirds of them (48 spp) into only 3 patterns (From Fig. 6 of McGowan & Walker, 1979).

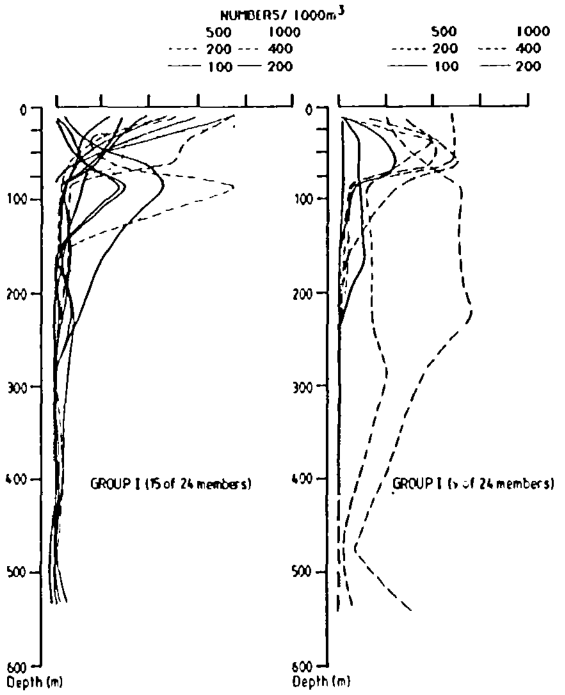

Fig. 3 Individual copepod species depth curves for the 24 species of Group 1 of figure 2. (From Fig. 19 of McGowan & Walker, 1979).

scales relevant to individual organisms, patterns may be seen that show species divide living space into discrete units that allow coexistence and thus explain the persistence of stable community structure. Within pattern at these scales, separation is sought in temporal partitioning of resource utilization and in specialization upon individual types of limiting resources or upon small portions of a resourch gradient (e.g., Boxshall, 1981). By extension, it can be argued that such specialization within habitats would provide a mechanism for creation of species distribution limits through the lack of flexibility to adapt to changing (or different) conditions within or between habitats. Few data are available to test this argument, but studies of copepods in highly diverse communities (for example, in very old, stable ecosystems like the North Pacific Central Gyre: Hayward & McGowan, 1979; Hayward, 1980; McGowan & Walker, 1979; 1985) show that they have not evolved temporal or spatial specialization in their patterns of resource utilization.

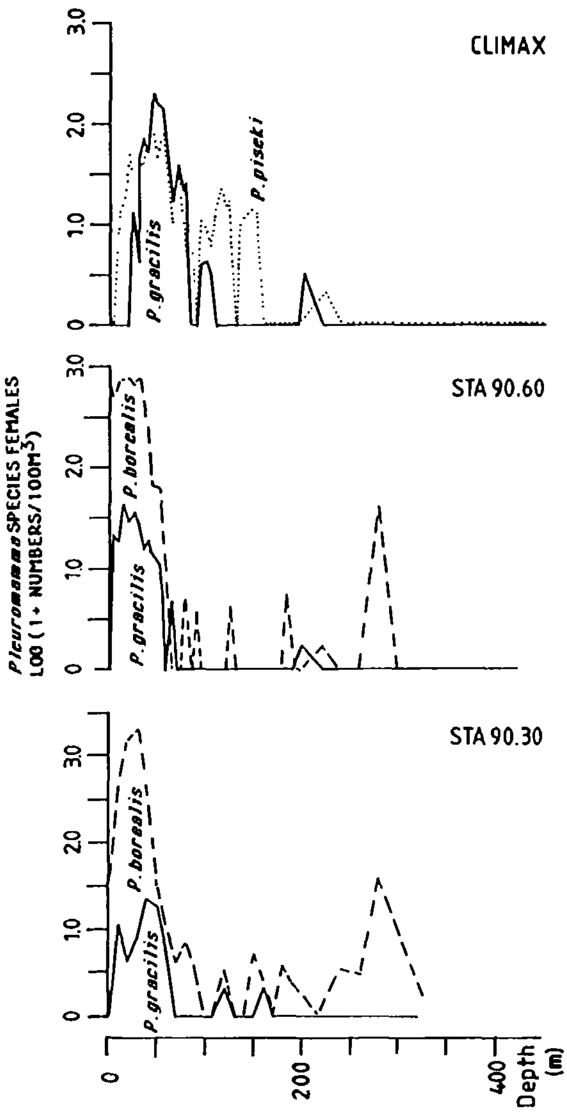

Fig. 4 High resolution (Longhurst-Hardy Plankton Recorder) sampling in the North Pacific central gyre and California Current showing the absence of separation by depth of morphologically similar species of the copepod genus *Pleuromamma*. Station positions are: 90.30, coastal Southern California (33°25'N, 117°54'W); 90.60, offshore California Current (32°25'N, 119°58'W); Climax, North Pacific central gyre (28°N, 155°W). (Haury, unpubl. data).

As a consequence of this lack of separation and/or specialization at the micro-and fine-scale

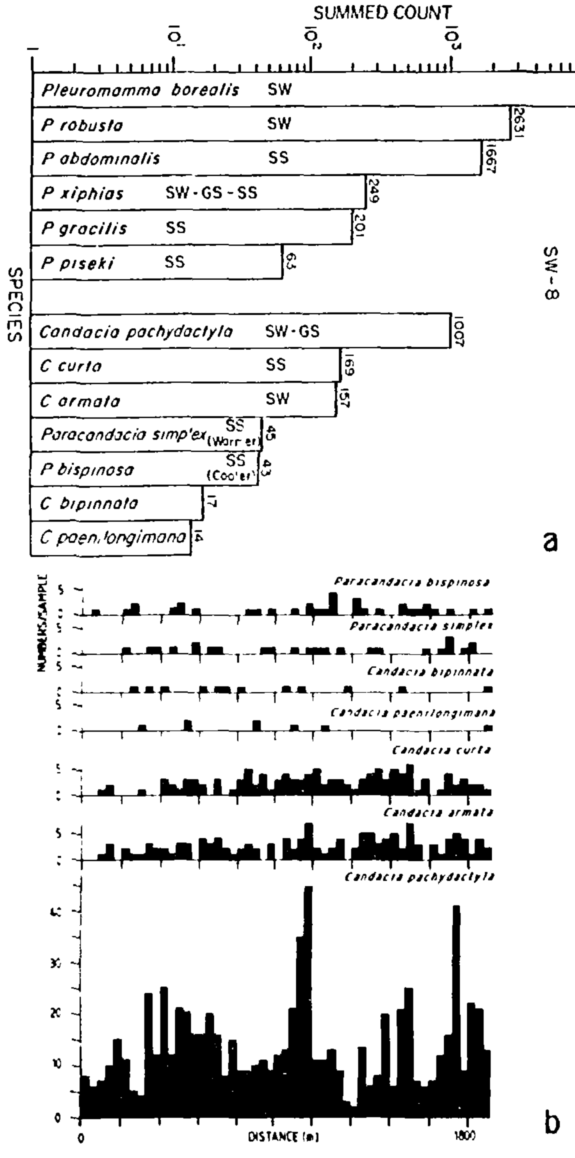

Fig. 5 Co-occurrence of closely related copepod species characteristic of various water masses within a small region of well-mixed water between North Atlantic Slope water and a Gulf Stream warm core ring. Samples collected with a Longhurst-Hardy Plankton Recorder at a depth of 35 (± 1m), temperature of 20.33 (± 0.03°C), and salinity of 34.37 (± 0.01). a) Horizontal distributions of species over about 1800m of tow; b) histograms of total abundance of two groups of related species. Species affinities are denoted by: SW= North Atlantic Slope water; SS= Sargasso Sea; GS= Gulf Stream. (Haury, unpubl. data).

levels, it appears that studies at this scale may be of little use to document mechanisms governing biogeographic limits based on niche concepts, resource partitioning, etc. The interactions between species that do go on at this scale could be of importance in determining the outcome of the mixing of water masses containing different communities, but these may very well be predictable solely on the basis of physical processes and the physical/chemical composition of the resulting water mass. That physical mixing and stirring can bring diverse planktonic communities together into homogeneous biological structures is shown in figure 5.

I believe the proper scale of studies to understand biogeographic boundaries and their stability should be kilometers to 100's of kilometers horizontally and 10's to 100's of meters vertically. These studies should be conducted in two general areas: 1) within the core regions (McGowan, 1974) of the principle oceanic communities and 2) across the transition zones between those communities that are characterized by reasonably sharp physical gradients but generally indistinct community (species replacement) gradients.

The concept of biogeographic core regions is directly related to the idea that several fundamentally different oceanic ecosystems exist. In core regions it is probable that the long-term average character of processes (including the variance and probability of extrema) provides the control, and not the small-scale temporal and spatial features. Understanding the regulating processes in core regions and how they differ between oceanic ecosystems, then, is a prerequisite to obtaining an understanding of factors which mediate community gradients between core regions. Such studies should therefore be of a long-term nature, concentrating on variability in community structure associated with things like the meso-scale eddy field and inter-annual variations in the large-scale physical/chemical field.

In the transition zones between core regions and in large ecotones like the California Current, it is not at all clear what the structure of community gradients is really like. As Boltovskoy and Angel (both in this volume) and McGowan (1971; 1974) have pointed out, the species making up a biogeographic unit in one place (core region) do not uniformity drop out across obvious physical gradients. That is, many species do not react in the same way to physical boundaries. Because most studies of biogeographic gradients at core region boundaries have been done at scales too large to resolve distributional changes in relation of physical features, it is not at all clear whether all species distributional limits can be correlated with front-like features or whether sharp community boundaries that have been observed at places like fronts are the exception, not the rule, when entire ecosystems are considered. Detailed studies of the relationships of community structure to physical structure on the coarse- to meso-scale would thus seem essential to resolve processes within gradient regions. Temporal aspects may also be important here, especially to address questions about the variability of boundary structures.

SAMPLING IMPLICATIONS

Within biogeographic core regions, it is probably at the meso-scale that the important interactions between species and between the community members themselves and physical features and processes will occur. The continuous nature of the patch structure within core regions suggests it is essential to sample as continuously as possible over scales ranging from several kilometers to 100's of kilometers. In transition zones, without prior information on the location or intensity of physical/chemical gradients, continuous sampling to scales of 100's of meters would be required to insure adequate resolution of the structure of community gradients.

A wide size range of organisms should be sampled as well, since the potential biological interactions between size classes are just as important as biological/physical interactions. It is essential to include nektonic organisms because they are less dependent upon physical features and are important predators upon the smaller size classes.

Other types of studies will be necessary, but are probably not possible on any scale approaching that recommended above. Knowing distributions (presence/absence or relative abundance) and associated environmental parameters alone will not lead to an understanding of mechanisms. Coarse-and meso-scale variability in fecundity, growth rates, behavioral traits, potential for genetic exhange (Bucklin, Marcus; this volume) etc., may reflect the mechanisms determining a species success in a particular environment or particular environmental and biotic gradient.

All these sampling goals are not new to biological oceanography and have been used to study other problems. The challenge to biogeographers is to employ them on the large scale necessary to bring progress to the field. I hope the arguments presented here help direct limited resources towards those scales which may produce the greatest advances in understanding.

ACKNOWLEDGEMENT

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VARIABILITY IN PRODUCTION AND THE ROLE OF DISTURBANCE IN TWO PELAGIC ECOSYSTEMS.

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INTRODUCTION

Environmental heterogeneity and the resulting variability in primary production and in the standing stocks of phytoplankton and zooplankton in pelagic ecosystems may have an important effect upon planktonic species structure and, thus indirectly, upon biogeographic patterns. The intensity and scales of heterogeneity (in the sense of Pielou, 1974) and the biological response to it are of particular interest here. The magnitude of patchiness in populations is an index of the strength of the biological response of the system to environmental perturbations; the scale of the response determines what fractions of the populations are affected and what the ecological consequences may be. Environmental heterogeneity may affect the outcome of interspecific interactions (DeMott, 1983) and it may determine the relative importance of physical and biological processes in affecting species structure. The question to be dealt with here is whether biological processes (interspecific interactions) or physical processes (variations in environmental structure) are likely to be of greater importance in affecting species structure. Interspecific interactions are assumed to be of relatively greater importance where the environment is "sufficiently" stable. This may lead to insights into the extent to which the range of a species and its patterns of abundance (and thus biogeographic patterns) are influenced by interspecific interactions.

Perturbations on certain spatial and temporal scales can a-priori be expected to have a disproportionate affect upon community structure. The most significant scales in the regulation of species structure are set by the biological characteristics of a species rather than by physical processes. The important temporal scales are related to critical periods in the life of an individual; such as the generation time (Hutchinson, 1961), the time from hatching to first feeding (Lasker, 1975), or the time from last feeding to starvation (Dagg, 1977). The important spatial scales reflect the ambit of an individual over these critical periods (Richerson et al., 1970). These scales depend upon the size and trophic status of the taxon, and they thus differ greatly for phytoplankton, macrozooplankton and nekton. Physical scales that roughly correspond to the mesoscale (tens to hundreds of kilometers) are likely to be especially important for macrozooplankton and nekton because this scale is of the same order as their ambit.

The intensity of environmental heterogeneity is also important. Central to this argument is the hypothesis that interspecific interactions will be the major determinant of species structure when and where the environment is sufficiently stable to permit this. That is, a "steady-state" set of species proportions should be reached in a invariant environment; although this need not be a unique set and a limit cycle could be reached. The question is whether heterogeneity in the environment perturbs the expected "steady-state" species proportions faster than the rate at which the actual species proportions approach "steady-state". If the environment varies in space or time faster than the biotic system can respond, then steady state with possible local extinctions will not be reached (Caswell, 1978). The potentially great importance of interspecific interactions in planktonic ecosystems is supported by observations in lakes that competition and predation can dramatically alter species proportions and even result in local extinctions over the course of a single season (Sprules, 1972).

In this paper I compare patterns of production and standing stocks in the central North Pacific and California Current ecosystems in order to ask whether these environments are sufficiently stable so that interspecific interactions are likely to have a major role in determining species structure. The discussion focuses upon macrozooplankton and nekton populations because the sampling scales were too large to assess the affects of environmental heterogeneity upon microplankton. The pelagic biogeography of the North Pacific and the roles of advective and in-situ processes in the regulation of species proportions have been reviewed elsewhere (McGowan, 1974; 1977).

METHODS

The data shown here were collected, using standard methods, on a number of different cruises (Hayward et al., 1983, Scripps Institution of Oceanography, 1985). Data from the May 1981 CalCOFI cruise are considered in detail because a set of within-station replicate samples was taken. Chlorophyll, extracted in 90% acetone, was measured with a fluorometer. Primary production was measured as ^{14}C uptake in half- day (local apparent noon to sunset), simulated in-situ incubations. These data are presented as vertical integrations through the upper 200m and the euphotic zone (surface to ~0.5% light level) respectively. Macrozooplankton was sampled with either a 1m diameter ring net or a 70cm bongo net. In both cases the mesh size was 0.505mm, and the nets integrated the upper 200m of the water column. Biomass data are presented as wet displacement volume. The same techniques were used in both ecosystems in order to allow comparison of the absolute values of these properties as well as the levels of variability.

OBSERVATIONS

THE CENTRAL NORTH PACIFIC

Variability in the given biotic properties is low on all spatial and temporal scales in the central North Pacific (Hayward et al., 1983). Within-station variability over two or three days is typically a factor of two or three. Meso and large-scale spatial variations and interannual temporal variations are seen, but they are scarcely greater in intensity than small-scale variability (Table I).

We can also ask if the spatial and temporal variations in these properties are intercorrelated and, if so, on what scales. A lack of correlation should amplify the affects of patchiness. Chlorophyll and primary production are intercorrelated over large spatial scales within a single cruise (Hayward & Venrick, 1982). The large-scale spatial patterns of chlorophyll, primary production and macrozooplankton biomass in the central North Pacific are generally similar (Hayward et al., 1983; unpubl. data). Mesoscale variations in chlorophyll and macrozooplankton biomass, however, do not appear to be correlated. This latter observation can not be statistically tested due to the design of the sampling scheme.

The interannual variations in chlorophyll, primary production, or macrozooplankton at a single station are all uncorrelated (Fig. 1). This is surprising given the good correlation between the spatial distributions of integrated chlorophyll and primary production. However, other data (Bienfang & Szyper, 1981; Bienfang et al. ,1984; Ohman et al., 1982) also show that, in the area near Hawaii and in the eastern tropical Pacific, the vertically integrated values of chlorophyll and primary production are uncorrelated on a time scale of months or on the mesoscale. These observations imply that the system is at least slightly removed from trophic steady-state on annual to interannual time scales. However, perturbations from steady-state are small, at least in terms of production and standing stocks.

THE CALIFORNIA CURRENT

The small-scale, within-station variability in primary production and standing stocks in the California Current is similar to that in the central North Pacific (Table I). Variability on meso and larger spatial scales is much greater. The contrast with the central North Pacific is greatest in the intensity of the mesoscale patchiness. Seasonal and interannual variations are also greater in the California Current than in the Central North Pacific.

Table I Estimates of the biological variability on various spatial and temporal scales in the Central North Pacific and California Current. Within-station variability is that at a single station (< 10 km) over a few days. Mesoscale is tens to hundreds of kilometers, and large scale is hundreds to thousands of kilometers. These are subjective estimates based upon an examination of the available data. Insufficient data exist to estimate the interannual variability in chlorophyll and primary production in the California Current.

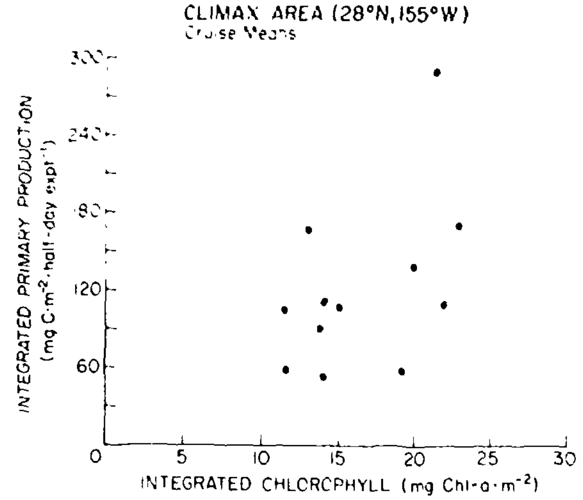
	CENTRAL NORTH PACIFIC		
	Chlorophyll	**Primary Production**	**Macrozooplankton Biomass**
Space			
Within station	<2	2-3	1.5-2
Meso-scale	2	2-3	2-3
Large-scale	2	2-3	3-4
Time			
Diel	1	---	1.5
Seasonal	<1.5	<1.5	<1.5
Interannual	2	3	1.5
	CALIFORNIA CURRENT		
Space			
Within station	<2	2-3	2-3
Meso-scale	5	10	50
Large-scale	10	10	10
Time			
Diel	<2	---	1.5-2
Seasonal	3-4	2-3	3
Interannual	?	?	5

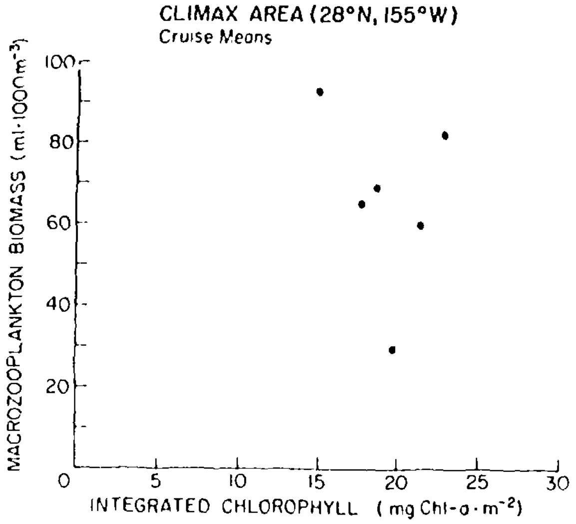
The meso and large-scale spatial distributions of chlorophyll, primary production and macrozooplankton biomass are intercorrelated within a single cruise, but there is considerable variability with this relation, especially for macrozooplankton biomass (Fig. 2). Chlorophyll and primary production, spatially integrated over the Southern California Bight, are uncorrelated on a time scale of months (Fig. 3). Macrozooplankton biomass and production are correlated on this time scale (Smith & Eppley, 1981).

Mesoscale patchiness in the California Current is the dominant feature. The contrast between patches and the area surrounding them may be a factor of 50 or more in the given properties (Fig. 4). Most of the standing stocks of phytoplankton and macrozooplankton are aggregated in a small fraction of the total area of the California Current (Fig. 5; Hayward, in prep.). There is a large area outside the patches that can be thought of as a "background". This background contains most of the area of the California Current but only a small fraction of the total standing stocks. The background area has standing stocks that are often not enriched with repect to the central North Pacific, and this area thus may itself be much closer to a trophic steady state.

DISCUSSION

What effects are these patterns of variability in production and standing stocks likely to have upon planktonic species structure in these ecosystems?





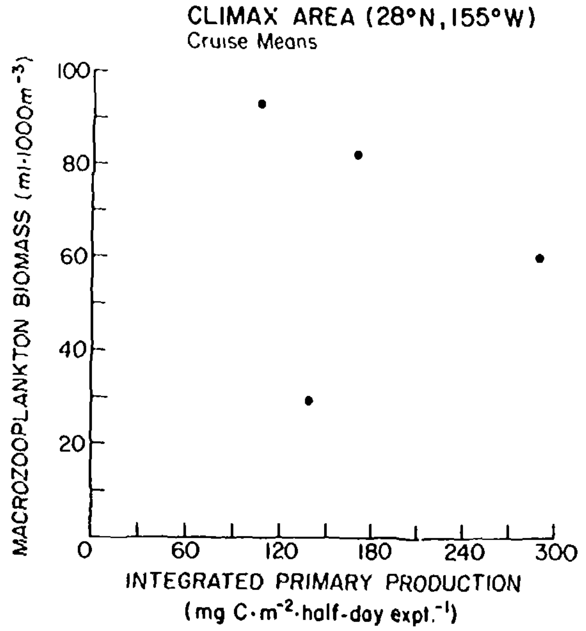


Fig. 1 Plots of the interannual variability in the relation between vertically integrated chlorophyll, primary production and macrozooplankton biomass at a single location in the central North Pacific (28°N, 155°W). Each point represents the mean value of the given property on a single cruise. None of these properties are correlated at the 0.05 level.

Is the environment sufficiently stable, and on what scales, so that interspecific interactions have an important effect upon the species structure?

Heterogeneity in the relation between the distributions of the given properties shows that environmental variability is greater than indicated by patchiness in any single property. Patterns in an individual property are thus insufficient to fully describe the biological response of these ecosystems.

The low overall variability in the central North Pacific implies that the system is close to trophic steady state. This also suggests that the expected "steady-state" species proportions do not vary greatly. This, in turn, suggests that interspecific interactions play the dominant role in determining species proportions. The great stability observed in the species proportions of trophic levels including phytoplankton (Venrick, 1982), macrozooplankton (McGowan & Walker, 1979; 1984), and nekton (Barnett, 1983) is consistent with strong regulation of species structure. However, the processes which maintain

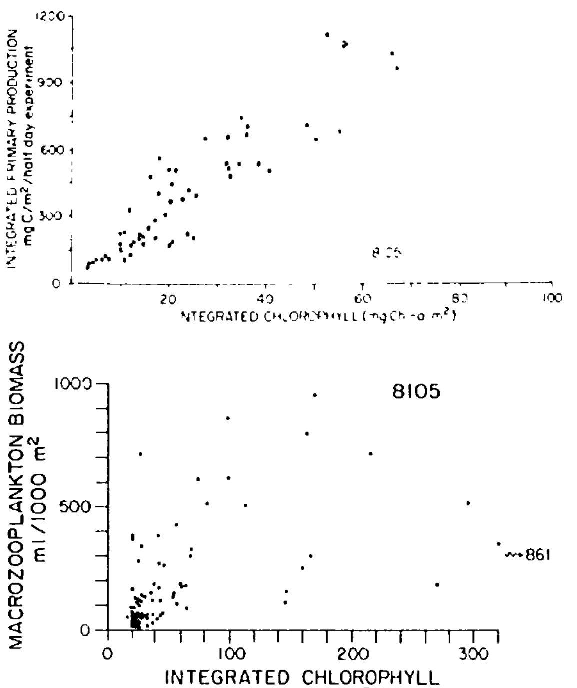


Fig. 2 Scatter plots of the spatial variability in intergrated chlorophyll versus integrated primary production and macrozooplankton biomass in the California Current on cruise 8105 (May 1981). Both relations are significantly correlated at the 0.05 level.

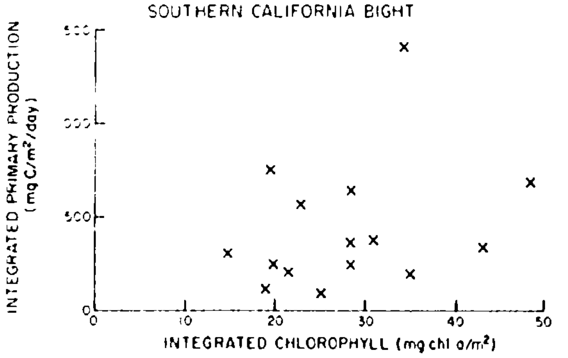


Fig. 3 Scatter plots showing the temporal variability in integrated chlorophyll and integrated primary production in the Southern California Bight region. Each point is a spatially averaged cruise mean. There is no correlation at the 0.05 level.

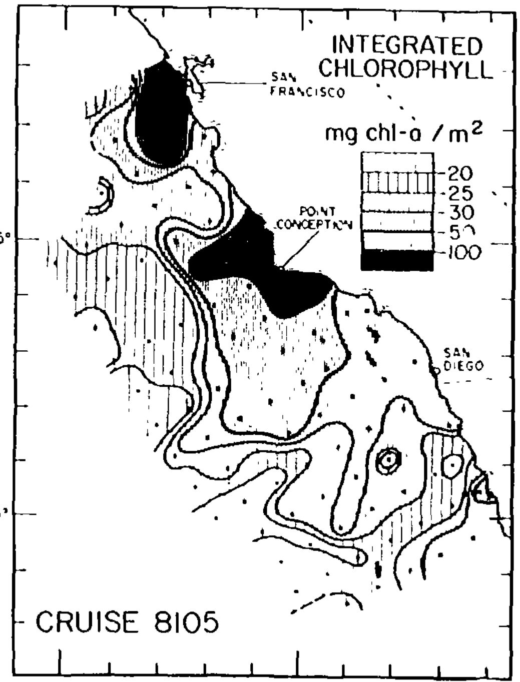
this stable species structure remain unclear (McGowan & Walker, 1984).

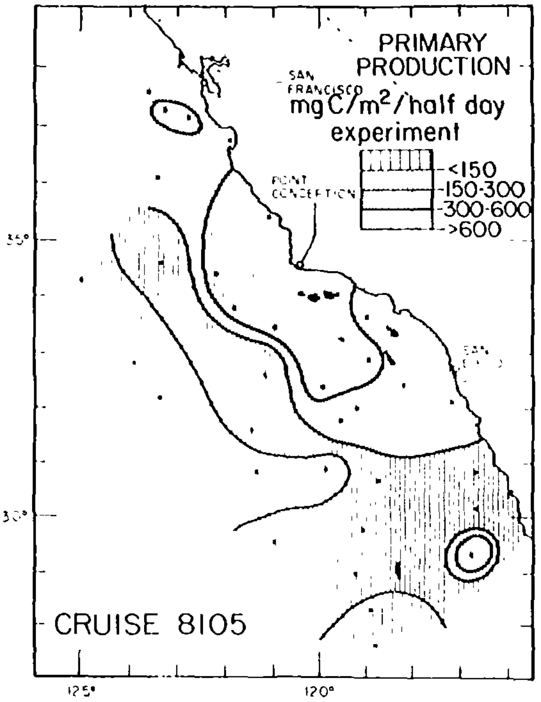
The way in which environmental variability affects species structure in the California Current may be more complicated. Variability on small (within station) scales is similar to that in the central North Pacific., and this is probably well within the range of individual adaption of the macrozooplankton and nekton. Variability on meso and larger scales is much greater than in the central North Pacific. Patches on these scales likely constitute different environments, and each patch could have a different expected "steady-state" species structure. Thus, the system as a whole is probably far from steady-state species proportions. The observed species proportions vary greatly from sample to sample (McGowan, 1974). This variability should decrease the relative importance of interspecific interactions in regulating the overall species proportions of this system.

The low correlation between the spatial distributions of chlorophyll and macrozooplankton biomass suggests that the area within patches is often far removed from trophic steady state. It is unknown whether the species structure within patches is close to steady-state. In order to assess the effects of meso and larger scale physical forcing processes it will be necessary to know more about the persistence of patches and the exchange rate of individuals and properties between them.

The background in the California Current may constitute an environment which is distinct from that in patches and which itself may be closer to trophic steady-state. The very low values of production and standing stocks suggest that this area has not recently been perturbed. If this is the case, the background in the California Current may be sufficiently stable so that interspecific interactions have a significant effect upon species proportions. It is thus also necessary to know more of the history of the water parcel from which samples are collected.

The low-frequency, large-scale variability in the California Current is associated with physical events such as El Niño (Chelton et al., 1982). Changes on this very large scale tend to be spatially coherent throughout the system.





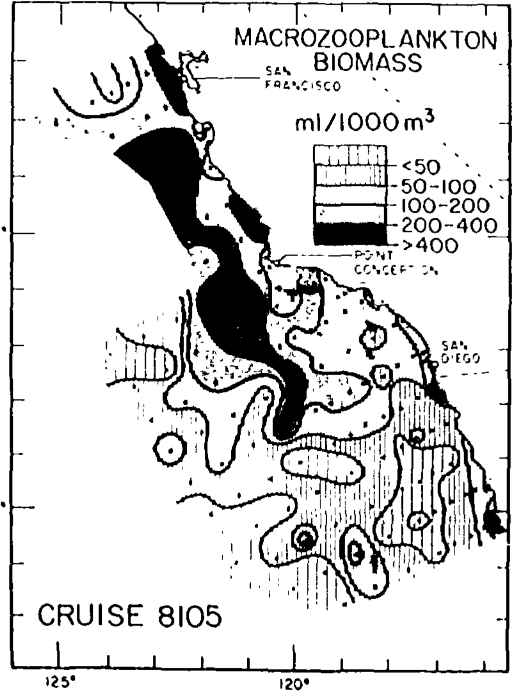


Fig. 4 Spatial distributions of integrated chlorophyll, integrated primary production, and macrozooplankton biomass in the California Current on CalCOFI cruise 8015 (May 1981).

Variations in the abundance and distributions of taxonomic groups (Colebrook, 1977) and individual species (Brinton, 1981) are also associated with environmental variations on this scale.

The species proportions in the California Current thus repond to both the in-situ structure of the system and external processes. A detailed examination of a single place or time is unlikely to represent the range of environmental conditions that the populations are exposed to over evolutionary time. Studies of in-situ structuring processes must consider the range of environmental variability in the California Current.

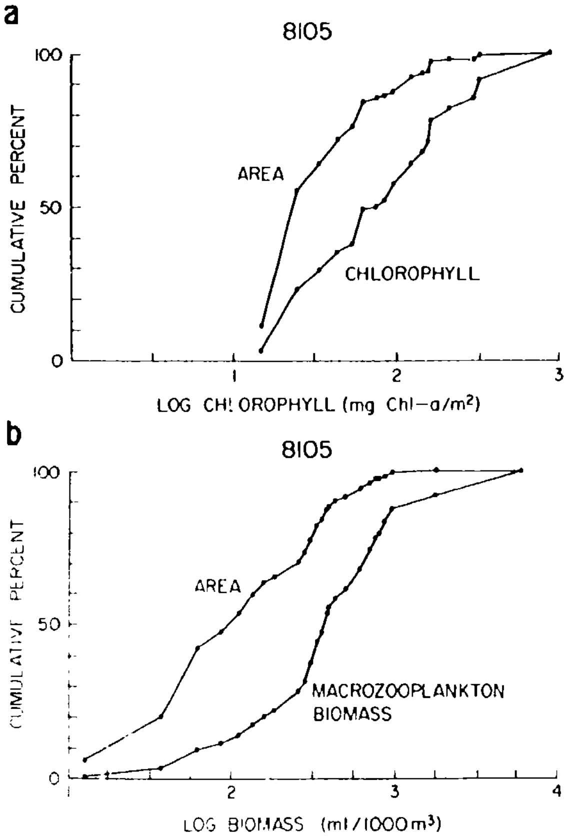


Fig. 5 (a) Summary of patchiness in the California Current on cruise 8105. The cumulative percentage of area is the fraction of the total area in the sampling grid (Fig.4) that has chlorophyll concentrations at or below that shown on the x axis. The cumulative chlorophyll is the fraction of the total integrated chlorophyll in the grid at or below that chlorophyll concentration. If chlorophyll is evenly distributed the curves will overlay. The difference in the curves shows the intensity of patchiness. For example, the 50% of the cumulative area with the lowest chlorophyll concentration has only about 20% of the total chlorophyll. To reach 50% of the total chlorophyll takes about 80% of the total area. This means that the other 50% of the total chlorophyll is found in the 20% of the area with the highest concentrations.
(b) Same as figure 5 (a) except for macrozooplankton biomass.

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MODES, TEMPOS AND CAUSES OF SPECIATION IN PLANKTONIC FORAMINIFERA

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INTRODUCTION

Calcareous shells of planktonic Foraminifera preserved in continous sedimentary sequences on the sea floor in areas of rapid sedimentation, above the calcite compensation depth (CCD) provide an excellent opportunity to test various hypotheses of plankton speciation including phyletic gradualism and punctuated equilibria (Mayr, 1963; 1970; Gould & Eldredge, 1977).

CAUSES OF EVOLUTIONARY DIVERSIFICATION

Bursts in evolutionary radiation have been attributed to the development of diverse habitats by continental fragmentation (Valentine & Moores, 1972), changes in land geography and in oceanic circulation, increased climatic zonation and decreased temperatures (Valentine, 1968; Lipps, 1970) as well as to higher and more uniform oceanic temperatures (Fischer and Arthur, 1977; Thunnell, 1981) more stable physical conditions (Tappan and Loeblich, 1973) and reversals in the Earth's magnetic field (Simpson, 1966).

The available geologic record provides evidence that in planktonic Foraminifera evolutionary diversification occurred when temperatures were fluctuating over extended time intervals, surface water temperatures were either increasing or decreasing, latitudinal temperature zonation was increasing or high, sea level was changing gradually and when continental fragmentation was proceeding at a slow and even rate (e.g. Herman, 1979; 1981 and references therein)(Fig. 1, Table I).

PLANKTONIC FORAMINIFERAL RECORD

Planktonic Foraminifera are unicellular marine protozoans possessing calcitic tests ≈30mμ - ≈1000mμ in diameter. Their abundance in marine sediments in depths from aproximately 200m to >4500m and the rapid evolution of some species make planktonic Foraminifera important in biostratigraphic zonation (e.g.Herman, 1979). Present-day distributional patterns show that most species are extremely sensitive to water-mass properties such as temperature, salinity and oxygen content, hence their usefulness as oceanographic and paleoceanographic indicators (e.g.Herman, 1979 and references therein).

GEOLOGIC DISTRIBUTION

Rare occurrences have been noted since Middle Jurassic, when small, globular forms, *Globuligerina*, were first recorded in marine sediments (Caron & Homewood, 1983). Evolving ggradually, planktonic Foraminifera reached their peak in the Late Cretaceous, whence several low and high diversity cycles are recorded; today they are represented by about 50 species (e.g. Herman, 1979). Following the terminal Cretaceous mass extinction, the morphologically simple globigerines survived giving rise to turborotaliids and globorotaliids (Cifelli, 1969), which diversified through the Paleocene reaching a peak by Late Paleocene (op.cit.; Table I), approximately 57.5my ago. The 62-57my period, was a time of fluctuating and warm deep and surface water temperatures, with ≈6-7°C differences between surface and bottom water values (Fig. 1). A decline in species diversity is recorded in Early-Middle Eocene (Cifelli, 1969;

Table I Causes of evolutionary diversification in planktonic Foraminifera

TIME in my	TECTONIC EVENTS	CLIMATIC EVENTS	OCEANIC EVENTS	PLANKTONIC, FORAMINIFERAL EVENTS	GENERAL
0					
0.9	Orogeny peak	0.9-0 Major glacial interglacial cycles Cenozoic Threshold IV	Arctic becomes perenially ice covered	In the Arctic initial appearance of present day assemblages	Onset of large amplitude climatic fluctuations
1.6			Northward shifts of Antarctic & Subantarctic watermasses Arctic CCD depressed.	PF diversity maximum Arctic PF has no analog in present oceans	
2.38			Arctic flooded with meltwater; development of low salinity SW	2.38-0.9 Arctic dominated by subpolar taxa	
2.4		Cenozoic Threshold III Initial major NH glaciation		2.4-0.9 Arctic Ocean mostly oligotrophic	Initial major NH glaciation followed by deglaciation
3.5	Uplift of Panama Isthmus	Gradual temp.decline			Development NH glaciation
5			Cooling of global DOW 5-2.4 Arctic SOW & DOW oxygenated. CCD elevated	PF diversity increases	
5.5	Isolation of Mediterranean Sea		Regression	Temporal reduction in PF diversity	
6		Strong global cooling 6-4 Expansion of Antarctic ice-cap			Major expansion of Antarctic ice
11				11-1 Gradual increase in diversity of PF	
14		14-12 Major Antarctic ice build-up	14-11 Dissolution Climax		
17.5					17.5-15: III $\partial^{13}C$ peak

18			18-0 Numerous rapid, large amplitude fluctuations of SOW & DOW; warming trend of SOW & cooling trend of DOW	18-14 PF diversity fluctuates	18-14 Short-term wide amplitude temp. oscillations of SOW & DOW; gradual increase in contrast between B & S water temp.; ≈38 cold-warm changes in 4 my
22			Development of Antarctic convergence		
24	Drake Passage opens	24-14 Increased glaciation of Antarctica; intensification of global climatic gradients	24-5 Transgressions; 24-18 Minor changes in SOW & DOW temps.	24-14 Gradual increase in PF diversity Major change in global planktonic biogeography to form latitudinal belts of assemblages from tropics to poles	
25			25-22 Development of unrestricted circum-Antarctic current creating the thermal isolation of Antarctica; expansion of sea-ice; increased vert.& horiz. oceanic circulation		
31				31-29 Major extinctions followed by evolutionary appearances	
35			35-18 SOW & DOW stable regime		
36.6	Greenland separates from Europe; Tasman Sea-way opens	Antarctic glaciation Cenozoic Threshold II	Abrupt cooling of DOW	36.6-24 Stable species diversity; gradual increase Reduction of PF diversity; diversity minimum; destinctive Antarctic faunal provinciality develops. Globigerines dominate	36.6-23.7 Lowest oceanic faunal & floral diversity for entire Cenozoic in Oligocene: low diversity gradients between low & high latitudes. Regression, end of warm polar climate

Table I (continued)

TIME in my	TECTONIC EVENTS	CLIMATIC EVENTS	OCEANIC EVENTS	PLANKTONIC, FORAMINIFERAL EVENTS	GENERAL
37			Short, conspicuous temp fluctuations; DOW temp. drop; SOW increase; initiation of thermohaline circulation; rapid drop of CCD; regression; SH sea ice	Diversity decreases	37-35: II ∂^{13}C peak
37.5			Abrupt, major DOW cooling, SOW warming		
40		Gradual cooling		40-37 Diversity high, several major extinctions followed by evolutionary appearances	
44			44-40 Gradual cooling of DOW, warming of SOW	44-40 Diversity maxima few major extinctions & appearances	
52				Diversity maxima,	
53	53-36 Labrador Sea & Baffin open		Flooding of Atlantic Ocean with Arctic water	Rapid decrease starts	
55	55-38 Australia moving northward		55-37 DOW & SOW gradual cooling underway; Atlantic DOW circulation; DOW & SOW cooling commences		
57				Diversity maxima 57-53 Decline in species diversity	

60					60-59: I ∂^{13}C peak: biological production maximum
62			62-57 Fluctuating warm DOW & SOW temps.		
65	Tasman Sea opens; Central Tetkys narrows. S.L. drops	65-62 Gradual warming	65-62 Gradual warming	Gradual evolutionary diversification of PF commences	
67	Continents reach polar position	Cenezoic Threshold I; Abrupt, large amplitude cooling	Presumed change in water chemistry; regression; abrupt large amplitude cooling	K/P boundary event; mass extinction of taxa at the peak of their evolutionary development	Selective mass extinctions
70			Transgression		

* Ages of events are approximate

Abbreviations:

BOW= bottom ocean water; DOW= deep ocean water; SOW= surface ocean water; NH= northern hemisphere; SH= southern hemisphere; CCD= carbonate compensation depth; PF= planktonic formaninifera; SL= sea level

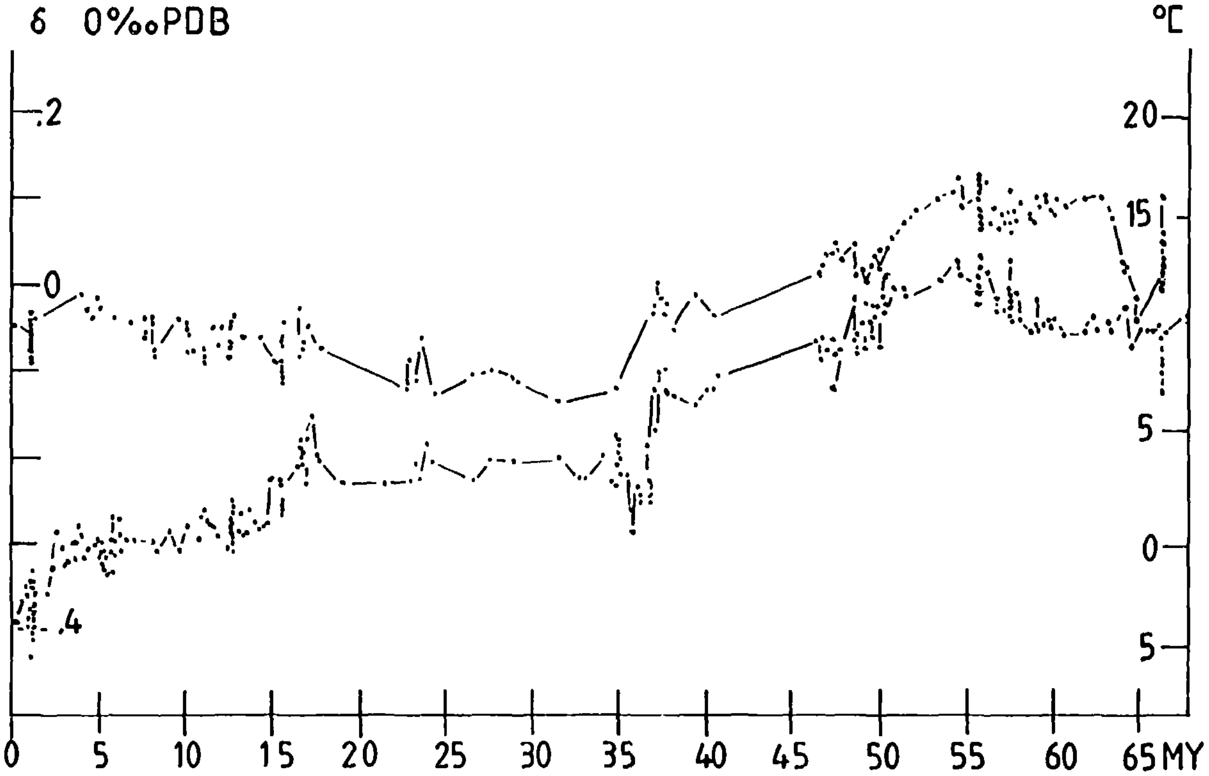

Fig. 1. Cenozoic oxygen and carbon isotope data of benthonic and planktonic Foraminifera, South Atlantic Ocean (from Shackleton et al., 1984).

Berggren, 1971) centering around 58-50my B.P., and following a $\partial^{13}C$ maximum, which presumably indicates high surface water biological production (Fig. 1). Another radiation is recorded between ≈44 and ≈37 my ago, interrupted by extinctions 40mya, 38.2mya and 37.3mya (Keller, 1983). Recent foraminiferal studies indicate that with the exception of the Eocene/Oligocene (E/O) boundary, these major faunal extinctions are abrupt events being followed by first appearances (Keller, 1983). This time interval is characterized by a gradual cooling of surface and deep water (Fig. 1, Table I); the trend is interrupted by a warm pulse centering around 38 my. A sudden major cooling event of the bottom water has been recorded at about 37my B.P. (Kennett, 1978; Keller, 1983)(Fig. 1), but the opposite trend occurs in surface water (Fig. 1). Sharp, short-term temperature fluctuations, by approximately 7°C were measured between ≈37-35 my B.P. (Fig. 1). The gradual E/O extinctions are much less severe than the terminal Cretaceous mass decimation of the calcareous microplankton (Keller, 1983). As in the Paleocene morphologically simple globigerinids survive and diversify (op.cit.). The next major radiation commenced in Miocene culminating by Middle Miocene, ≈15my ago. However, a number of fluctuations in foraminiferal diversity were recorded between ≈17 and 12my B.P. By the end of Early Miocene fully-keeled globorotalids were diverse, orbulines and hastigerines had also evolved; the pulleniatines appear in Late Miocene (op.cit.) From Middle Miocene on, the planktonic foraminiferal faunas are essentially modern. During the last 1.7my, numerous temperature fluctuations are recorded (Fig. 1)(Keller, 1978; Herman, 1979 and references therein).

MODES AND TEMPOS OF EVOLUTION

Several modes of speciation have been suggested for oceanic microplankton, they include: 1. Phyletic gradualism, whereby new series arise through gradual and continuous phyletic transformation within the population of an entire species. This process is believed to proceed at a slow and constant rate; 2. Punctuated equilibria, whereby evolution is concentrated in very rapid events, considered instantaneous in terms of geologic time. This second model is believed to occur in genetically isolated or semi-isolated populations at the outer fringes of the geographic range of ancestral species, followed by migration to other areas (allopatric speciation of Mayr, 1963; 1970; see also Gould and Eldredge, 1977); and 3. Punctuated gradualism, described by Malmgren et al. (1983). According to these authors, evolutionary steps could take place within a bioseries in one region, without migration of newly evolved species (op.cit., Malmgren and Kennett, 1981). Furthermore, new species evolve not through lineage branching as required by punctuated equilibria through periods of rapid, but not instantaneous, phyletic transformation of entire populations (Malmgren et al., 1983). In an interesting study Malmgren and his collaborators (ibid) have analyzed the lineage of warm water *Globortalia tumida* through the last ten million years of its evolutionary history in a southern Indian Ocean core. This lineage is believed to be predominantly of Indo-Pacific origin and distribution (op cit). The evolutionary sequence leads from *G.merotumida* -> *G.plesiotumida* -> *G.tumida*, with no evidence of divergence in this lineage (op.cit.). The material studied, from DSDP Site 214 in water depth of 1665m was selected because of the shallow water, well above the lysocline, consequently these dissolution resistant species were very well preserved. Sampling interval was between $5x10^3$ yrs and $15x10^3$ yrs across the Miocene/Pliocene boundary (5.3my) and $2x10^5$ yrs in the remainder of the section. Various morphological characters were measured. The results indicate that during the Late Miocene the *G.plesiotumida* populations were in stasis for ≈5my. About 5.6my ago the test shape began to change gradually completing the transformation to *G.tumida* in about 0.4my, remaining essentially unchanged since that time. These authors have demonstrated that at least in the *G.merotumida* - *G.tumida* lineage "punctuated gradualism" is the speciation mode. In another investigation, Malmgren & Kennett (1981) recognized a case of phyletic gradualism, without branching in the evolutionary lineage of *Globorotalia conoidea* -> *G.conomiozea* -> *G.puncticulata* -> *G.inflata*. Scott (1983) disputed this lineage and suggested that *G.conoidea* split and one branch gave rise to *G.inflata* in a relatively short time thus supporting the "punctuational" model of speciation (op.cit.).

Still a somewhat different ancestral-descendant relationship in these and related taxa is suggested by Berggren (1977 and references therein). To further complicate matters Arnold (1983) used the evolution of *G. crassaformis* from its ancestor *G.cibaoensis* via *G.puncticulata* as an example of "phyletic gradualism". Different opinions concerning ancestor-descendant relationships exist in may lineages, however, lack of space precludes a detailed discussion of this problem. The state of taxonomic chaos is exemplified by *Globigerina pachyderma* referred to by various other generic names including *Aristerospira*, *Neogloboquadrina*, *Globorotalia*, *Turborotalia* and *Globoquadrina*. This species is believed by seven pachyderma experts to have evolved either from the *Globorotalia opima-mayeri* group, or from *Globigerina angustiumbilicata*, or *G. continuosa*, or a turborotalid ancestor (in Kennett & Srinavasan, 1980 and references therein).

Before the challenging problems of causes, modes and rates of speciation can be addressed we need to sort out questions concerning taxonomy, phylogeny, paleoceanography and paleogeography.

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ON CURRENTS OFF NORTH-WEST AFRICA AS REVEALED BY FISH LARVAE DISTRIBUTIONS

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INTRODUCTION

Displacement by currents may affect the early life history of fish (see e.g. John, 1984a; Norcross & Shaw, 1984; Power, 1984; or literature cited there).

Investigations off Northwest Africa during the past twenty years provide enough knowledge to fulfill part of the requirements defined by John (1984a) for the assessment of larval drift for several species.

The broad scheme of German ichthyoplankton surveys off NW Africa is shown by figure 1. The subarea of particular interest (the "Mauritanian province"; Backus et al., 1977) has been thouroughly sampled (178 stations) from the surface to 150m depths. Additional samples outside of the Mauritanian province, applying identical methods, prove that peculiarities encountered are not due to sampling. Details of the cruises can be found in the literature (John, 1985; Andres & John, 1984). Unpublished results for selected species from "Meteor" cruise no. 64 (January- February 1983 off Morocco and Mauritania) and cruise no. 69 (October - November 1984, open subtropical NE Atlantic) are included here. Horizontal and vertical distribution patterns for fish larvae off Mauritania were presented by John (1985). The term "near-surface occurrence" refers here to vertical distributions shallower than 30m, "extended vertical distribution" to species ranging from near the surface to at least 60m, and "deeper distribution" to a maximum below 60m.

The existing charts of surface currents (e.g. Angel, 1979) generally show a flow towards the south-southwest for the area along Northwest Africa. The southward extension of range for the warm-temperate ichthyofauna along the coast to tropical latitudes (e.g. Maurin, 1968; Sedletskaya, 1983a) results from these currents. In the open ocean the Canary Current probably transports large numbers of *Macrorhamphosus scolopax* (Fig. 2) and lesser numbers of Synodontidae, Mullidae and Gadinae to the south and west of their bathymetrically and geographically confined birth places (John, 1973; Andres & John, 1984).

Detailed charts (e.g. Dhi, 1967) also show surface currents along the NW African coastal area south to Cape Blanc or, during the winter, to Cape Verde. Several examples show that near-surface taxa drift along the coast (John, 1984a); e.g. off Morocco during winter neritic species such as *Belone sretoridori* and *Sardina pilchardus* were confined to a zone less than 60

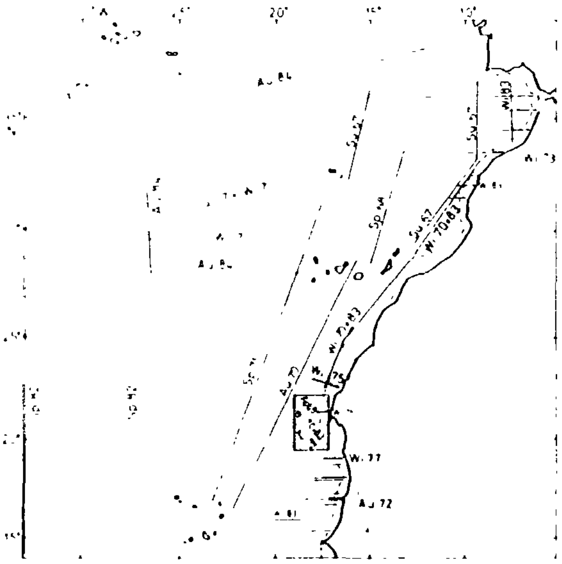


Fig. 1 Location and seasons of plankton sampling 1967-1984. Lines denote transects, hatched areas repeated sampling. Wi= winter Sp= spring Su= summer Au= autumn.

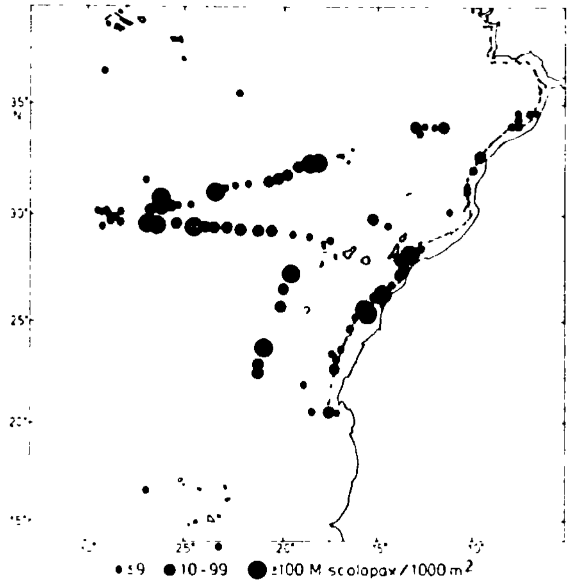


Fig. 2 Occurrences of planktonic stages of *Macrorhamphosus scolopax*. Shaded: known or bathymetrically possible (50-400m) spawning grounds. Interrupted: spawning grounds 20°N-23°N represent a southward extension of spawning 1975-1983.

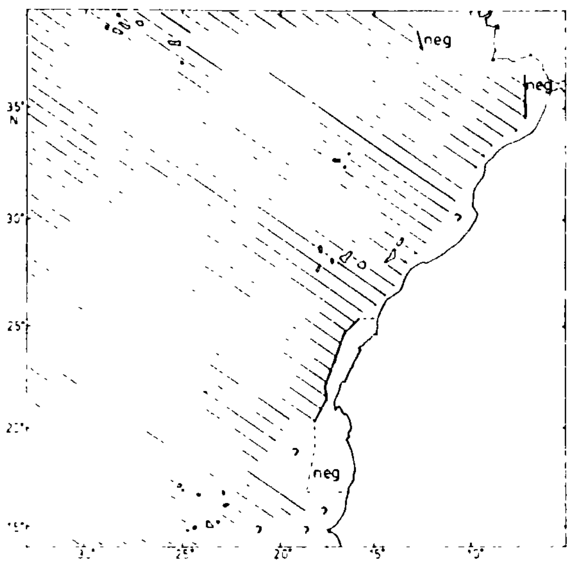


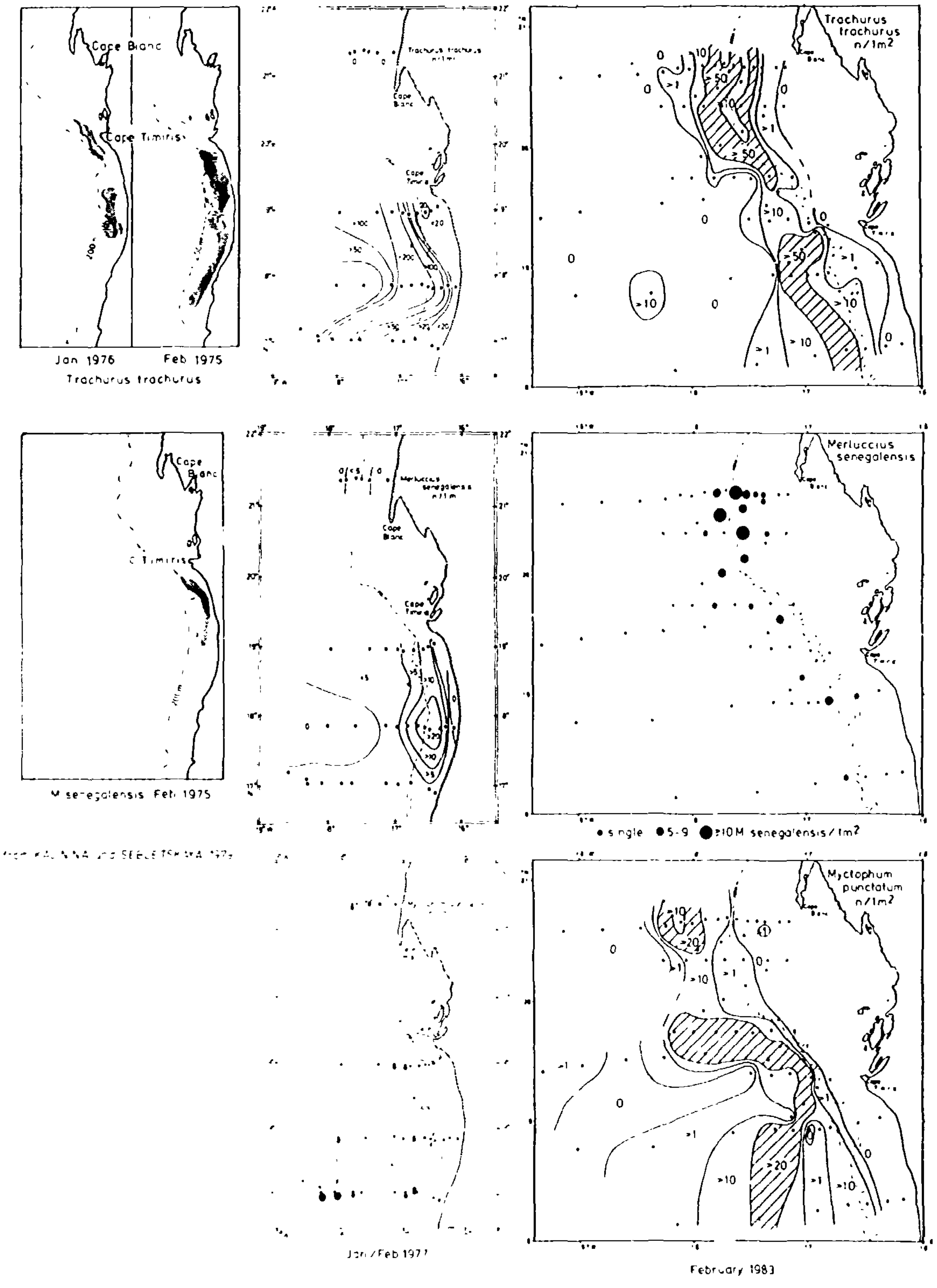
Fig. 3 Occurrences of surface larvae of the family Scomberesocidae (diagonally hatched). Solid lines denote limits of distribution, broken lines area where family was absent. Question marks refer to areas where data are not available.

nautical miles (n.m.) from the shore (John, 1979), while oceanic Scomberesocidae reached into this range (Fig. 3; see also John, 1979). Off West Sahara *Scomberesox saurus* was rare above the slope (John, 1973), but 70n.m. from the shore on average 3.2 larvae/1000m^2 were caught ("Meteor" cruise no.64).

Seasonal and regional changes in the direction of that current component normal to the coastline are known (e.g. Wooster et al., 1976). A shift of the trade winds results in offshore surface flow and an upwelling of cold water during late spring, summer and autumn of Morocco, where during the winter and early spring transport at the surface is either parallel to the coast or shoreward. Upwelling persists throughout the year between 25°N and 20°N, but only during winter and spring off Mauritania. During summer the coastal surface flow off Mauritania is northward and onshore. Data on the interannual variability are described by Sedykh (1978) and Michelchen (1984). The effect of a reversal of surface flow off Mauritania on the distribution of larvae was shown by Hamann et al.(1981).

Seasonal and interannual changes influence the species composition and abundance of ichthyoplankton (Sedletskaya, 1983a; John, 1973; 1985). Evidence for the effect of the reversal of surface transport normal to the coast upon the ichthyoplankton off Morocco is indirect. During upwelling sardine eggs are abundant even offshore of the spawning grounds, and an offshore and southward drift of sardine larvae occurs (Sedletskaya, 1983b). Off West Sahara, two examples for offshore drift in the surface layer are known (John, 1984a). Absence of *S. saurus* above the slope also must be due to the same effect (the species may occur above the slope off Cape Blanc, when water temperatures above 17°C are found, i.e. outside of the upwelling regime- see Hartmann, 1970).

More information about the Mauritanian coastal upwelling has now become available (John, 1985). These data allow an interpretation of the literature and preliminary results from a recent cruise, even though final hydrographic data are



from KALININA and SEELETSKAYA [illegible]

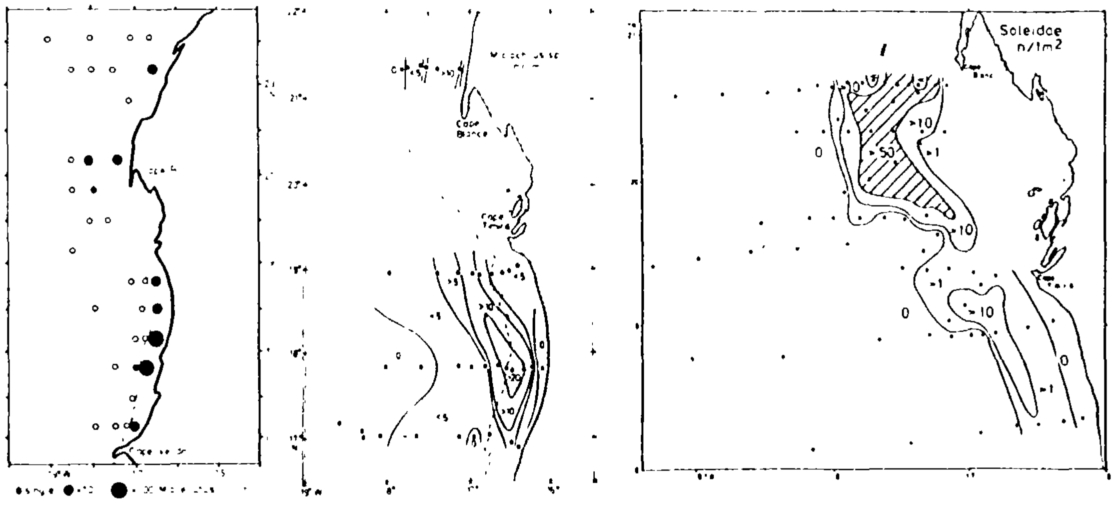
Fig. 4 Horizontal larval distribution patterns of 3 species with extended vertical distribution during different winters.

not yet available. The horizontal patterns of some species with extended vertical distribution (Figs. 4, 5) will be compared, as they represent almost all the mechanisms involved. Within this group, *Trachurus trachurus* spawns above the mid-shelf. Vertically, consistently more than 50% of the larvae occurred in the upper 30m and neuston tows yielded high numbers. These larvae should be most affected by drift of surface waters.

Consequently, larvae occurred above the spawning places when upwelling was low (data by Kalinina & Sedletskaya, 1979, see Fig. 4), and closer to the spawning grounds, when, during a season of intense upwelling, the surface flow was reversed (1977 - 18°N compared with the other transects). From a multitude of distribution data for the years 1963 to 1983 on *Trachurus* (Wiktor, 1971; Killachenkova, 1970; Sedletskaya, 1975; Bendixen, 1977; Kalinina & Podosinikov 1978; Fig.4 for 1983), the above mentioned two patterns represent the extremes of nearshore and offshore occurrences so far described - and they come from years with very different upwelling intensities (Sedykh, 1978).

Myctophum punctatum is an oceanic to slope-spawning species, the larvae have a fairly even abundance from near the surface to 60m occurring also below 60m. During strong upwelling the deeper living larvae are carried onshore by water masses feeding the upwelling (Hamann et al., 1981), while during weak upwelling, shelf waters are devoid of larvae (Bendixen, 1977)(Fig. 4 for 1983). Another example has been given by John(1985) for deep *Bathylagus* larvae.

While both near-surface neritic (see as well other examples by John, 1984a; 1985) and deep living slope or oceanic larvae reveal transport normal to the coast correlated with upwelling intensity, no such transport became evident for those larvae spawned above the shelf edge or upper slope and which have a maximum occurrence in the upper part of the undercurrent (e.g. *Merluccius senegalensis* and soleid genus *Microchirus* ; Figs 4, 5). In the literature additional data exist only for *M. senegalensis* (Kalinina & Sebletskaya, 1979) and Soleidae, and all these agree (Wiktor, 1971; Kalinina & Podosinnikov, 1978). It is therefore concluded that the distributions of larvae with known and restricted spawning areas are good indicators for currents. It is furthermore speculated that in the Mauritanian area larvae spawned at the shelf edge and upper slope which have an intermediate vertical distribution suffer little removal from adult habitats.



November 1972
after BENDIXEN 1977

Jan/Feb 1977

February 1983

Fig. 5 Horizontal distributions of larvae of deep-spawning soleids during three surveys.

Considering removal of plankton from its adequate environment, biologists have suggested recirculation models (e.g. Richert, 1975).

Mesoscale gyres (<120n.m. diameter), such as proposed by e.g. Mittelstaedt (1974) and Shaffer (1976), would help to explain recirculation even of organisms with a rather short planktonic phase, like that of some of the fish larvae encountered, but no biological evidence exists.

On the basis of repeated measurements of northward flow off the Mauritanian shelf, Mittelstaedt (1983: Figs 3, 4) proposed a gyral current which is partly supported by Stramma (1984). Though this gyre has too large a scale for a recirculation of fish larvae and the actual knowledge of hydrography might equally well be interpreted by a near-shore poleward and the oceanic southward Canary Current (Hagen, 1981; Hagen & Schemainda, 1984), it shows some striking congruence with ichthyogeography. The boundaries of the Mauritanian upwelling province agree fairly well with the extremes covered by this gyre, so that the existence of the province would easily be explained by a nearly self contained system in the epipelagic zone. The problem to identify larvae of the two myctophid species characteristic for this province (*Lampadena pontifex* and *Diaphus holti*) did not yet allow study of this question, but Krefft (pers. comm.) considers both the above to be slope species, whose reproduction might be favoured by the current system.

The distribution of neustonic Scomberesocidae has been given in figure 3, and reveals a consistent "scomberesocid hole" off Mauritania during the winters of 1970, 1977 and 1983 as well as the spring of 1968. The easternmost occurrences off Cape Blanc and at 16°N represent single larvae, suggesting only extreme limits of distribution. None of the other surface larvae considered typical for the tropical and warm-temperate open Atlantic (John, 1983) were found during these surveys, but during autumn 1972 plankton tows unlikely to catch surface species revealed the presence of some of them (Bendixen, 1977).

Surprising is the absence of larvae of the genus *Cyclothone* (Fig.6), since adults are regularly caught from the depths of the open ocean as well as above the deeper slope. Some few larvae, however, were caught in this "*Cyclothone* hole" during autumn 1972. As the larvae were always among the regularly caught taxa in adjacent areas, a seasonal cycle in reproduction off Mauritania seems less likely. Contrary to Scomberesocidae, *Cyclothone* larvae belong to the group with vertically extended distribution and a subsurface maximum (John, 1984b and literature there). The larvae should therefore be less affected by surface drift and occur farther to the east than Scomberesocidae. This is demonstrated by *Cyclothone* larvae above the shelf (above bottom depths of only 90m) between 31°N and 32°N (Fig.6), where upwelling took place. Contrary to this expectation however, off Mauritania, the easternmost occurrences were even farther to the west than for Scomberesocidae.

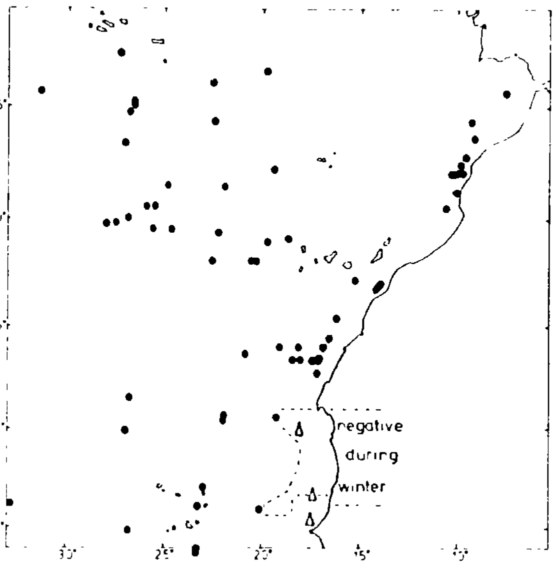


Fig. 6 Occurrences of larvae of the oceanic genus *Cyclothone*. Dots: Occurrences disregarding seasons. Open triangles: Occurrences only in autumn.

While several surface species are excellent indicators for surface drift, *Cyclothone* larvae in the Mauritanian province should be indicators for advection of near-surface (10? - 60m in eutrophic areas?) oceanic water masses. Patterns of relative abundance in the material under investigation (16°N - 21°N, coast to 20°W), combined with information on relative age, may prove if a connecting link exists between the Canary Current and the slope off Cape Verde. The offshore link proposed for south of Cape Blanc is not evident, unless offshore deflection of *M.punctatum* (Fig. 4 for 1983) is so interpreted. The latter conclusion is not convincing, as *M.punctatum* is an "oceanic" species.

The Mauritanian province is a promising area for the investigation of the effect of larval drift on ichthyogeography, it offers distinct peculiarities, adequate indicator species, good hydrographical data and biological material especially obtained to test existing theories.

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POLYTYPY, BOUNDARY ZONES AND THE PLACE OF BROADLY-DISTRIBUTED SPECIES IN MESOPELAGIC ZOOGEOGRAPHY

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INTRODUCTION

For those mesopelagic species whose distribution lies entirely within the warmwater regions of the ocean (ca. 40°N to 40°S), it is heuristically useful to distinquish two major distribution patterns (e.g. Brinton, 1962; Ebeling, 1962; 1967; Johnson, 1974; 1982):

1. species relatively restricted in distribution, limited to one ocean basin and generally limited to all or part of one water mass region (refers to geographic area underlain by a principal upper water mass as depicted by Sverdrup et al., 1942: 740).
2. species more widespread, with distributions crossing water mass boundaries, typically in two or three ocean basins, exhibiting varying approaches to warmwater cosmopolitanism (see Johnson, 1982: 185 for subcategories; also see Ebeling, 1967; Fleminger & Hulsemann, 1973).

Most attention in pelagic biogeography has focused on species relatively restricted in distribution and such focus has resulted in discovery of distinct and discrete open-ocean species assemblages, recognized by concordance in relatively restricted distribution of species from diverse taxonomic groups and trophic levels (Parin, 1970; McGowan, 1971; 1974; 1977; Johnson, 1982; Brinton & Gopalakrishnan, 1973; Backus et al., 1977). Such assemblages constitute the open-ocean equivalent of the "biotas" of the vicariance biogeographers (Croizat et al., 1974), but their study by open-ocean workers has been almost entirely ecological in orientation (Johnson, 1982: 174). The number of patterns ("ecosystems" in McGowan, 1971; 1974; 1977; "assemblages" in Barnett, 1983; "provinces - regions - distribution-patterns areas" in Backus et al., 1977) is apparently both finite and rather small.

BROADLY-DISTRIBUTED SPECIES

While there are broadly-distributed species that show within-ocean concordance with recognized species assemblage areas (Johnson, 1982; Johnson & Glodek, 1975), there are many broadly-distributed species that in contrast are widely-distributed throughout most of the tropical-subtropical area of all three ocean basins. For example Van Soest (1979) tallied data for 957 oceanic zooplankton species and showed broad to very broad distributions (crossing water mass boundaries) for two-thirds or more of the mesopelagic species for which he had data. Johnson (1974; 1982) showed that among 17 warm-water scopelarchids and evermannellids, six species, all in the Pacific, are restricted in the sense used above; three species, all equatorial, occur in just the Indian and Pacific Oceans (paralleling results of Fleminger & Hulsemann, 1973; Judkins, 1978; and others); and ten species occur in all three oceans. This proportion of three ocean species is by no means to these two families (see Gibbs et al., 1983: 119 for extensive documentation). It is sufficiently common that Ebeling (1967) recognized a catchall "Circumcentral-Tropical" Primary Zoogeographic Region incorporating all oceanic warm-water areas except the Mediterranean and eastern tropical Pacific. McGowan (1974: 15) lumped species broadly-distributed in the Pacific into a "Cosmopolite Fauna", broadly overlapping other recognized warmwater faunal regions.

Such "waste-basket" treatment typifies the "place" of broadly-distributed species in discussion of pattern in open-ocean distribution: they are essentially ignored. This results from at least three factors: lack of material, dearth of synoptic systematic studies world-wide in scope, and lack of conceptual framework, a set of working hypothesis regarding the "fit" of broadly-distributed species.

Barnett (1975: 36; 1984: 207) presents a plausible framework of ecological / biogeographical hypotheses relevant to broadly - distributed species and cites possible examples (Table I). In the present paper only the "eucosmospolite" category is considered. Here the working hypothesis is that broadly-distributed species are comprised of separable, genetically-distinct populations, the differences reflecting adaptation, and, that replacement of these populations occurs at the boundary of species-assemblage areas. This concept is not new (e.g. Brinton, 1962; 1975; McGowan 1971; Johnson & Barnett, 1975; Badcock, 1981; Johnson, 1982), but two major difficulties have precluded thorough documentation: lack of adequate sampling coverage-horizontally, vertically and temporally; and secondly frequent inability to distinguish ecophenotypic effects from differences related to genetic divergence (Brinton 1962: 178; 1975: 210).

THE HYPOTHESIS OF POLYTYPY

Reflecting these problems is a study of meristic character variation in broadly-distributed meso-pelagic species, selected on the basis of occurrence throughout the broadest possible range of warm-water oceanic habitats (Johnson & Barnett, 1972; 1975). Values for selected meristic characters and three measures of "food

Table I Categories of broadly-distributed species, with putative examples of each category (modified from Barnett, 1975, 1984)

1	**ECOLOGICAL OPPORTUNISTS** **Build up large populations only in ecotonal areas**
2	**SPECIES "BUFFERED" BY DISTANCE FROM PRIMARY PRODUCERS** **High trophic level carnivore, filter = trophic distance** ***Chauliodus sloani, Echiostoma barbatum, Leptostomias haplocaulus, Odontostomops normalops, Stemonosudis macrura, Avocettina infans*** **Bathypelagic zooplanktivore, filter = vertical distance** ***Poromitra crassiceps, Scopeloberyx robustus, S. opisthopterus, Taaningichthys bathyphilus, Lampanyctus niger***
3	**SPECIES EXHIBITING MARKED VARIATION IN ABUNDANCE FROM ONE ECOSYSTEM TO THE NEXT** **Abundant in gyres, present but rare at equator** ***Sternophyx diaphana, Argyropelecus hemigymnus, Cyclothone pallida, C.alba, Argyropelecus sladeni, Diaphus elucens, D. schmidti, Gonostoma atlanticum*** **Abundant at equator, present but rare in gyres** ***Hygophum proximum, Cyclothone acclinidens, Lobianchia urolampa, Danaphos oculatus, Nemichthys scolopaceus***
4	**"EUCOSMOPOLITES" BROADLY-DISTRIBUTED SPECIES NOT SHOWING MARKED VARIATION IN ABUNDANCE FROM ECOSYSTEM TO ECOSYSTEM** ***Notolychnus valdiviae, Lampanyctus steinbecki, Diogenichthys atlanticus, Ceratoscopelus warmingi, Symbolophorus evermanni, Triphoturus nigrescens, Vinciguerria nimbaria***

availability" were correlated negatively, but no relationship with temperature, salinity, or dissolved oxygen could be found. Ecophenotypy was argued against but could not be totally ruled out. Johnson & Barnett (1975) hypothesized that the observed variation is the result of adaptation of egg size, fecundity, and larval size to differing productivity conditions. They possessed only limited and indirect evidence for the last of the three predictions.

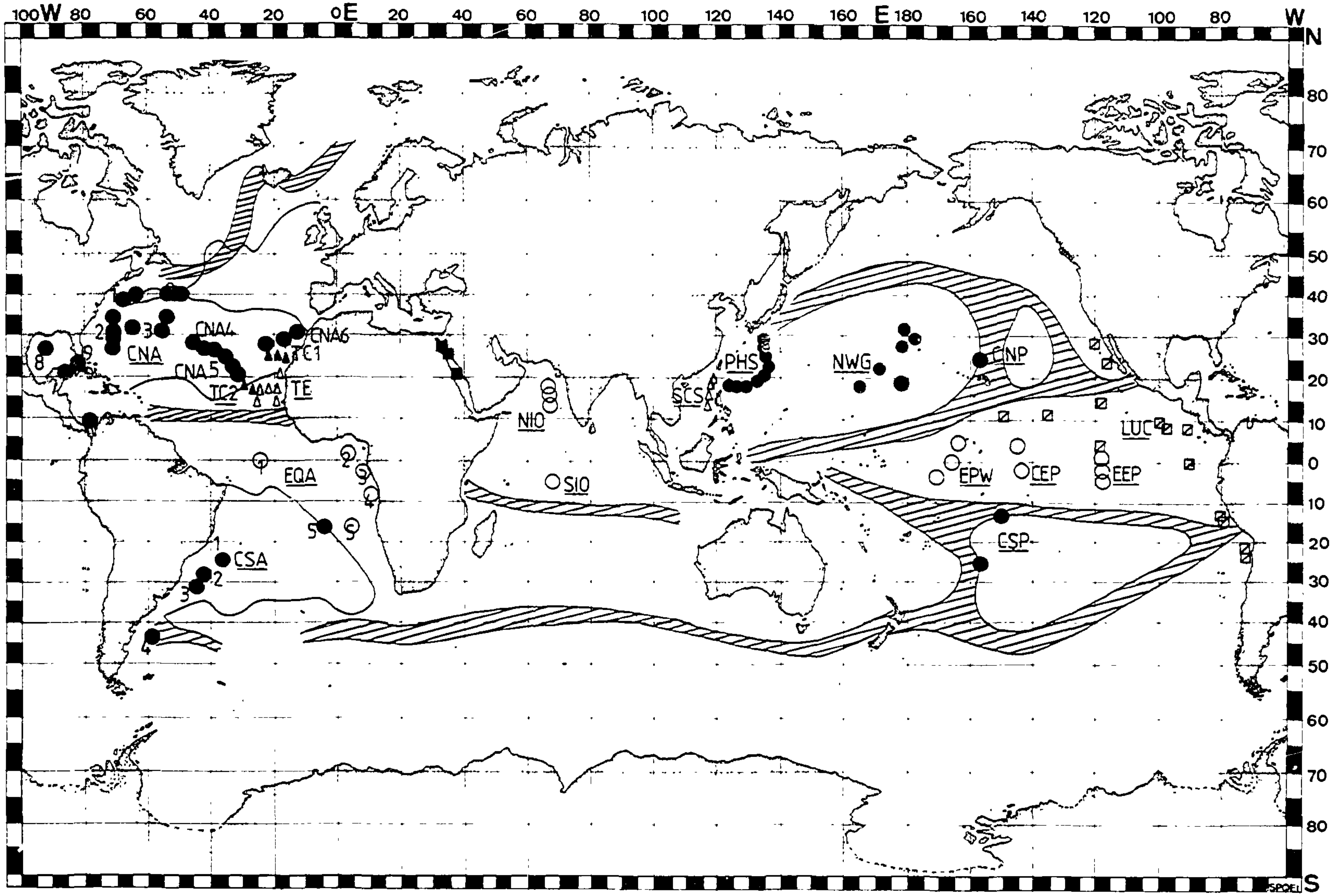
Relevant to the present paper is the hypothesis that the observed meristic variation reflects genetically distinct, allopatric populations of broadly-distributed midwater species and that the distribution of such populations is congruent with areas defined by the "generalized tracks" of assemblages of distributionally-restricted species. While the concept of polytypy is hardly novel by terrestrial standards, better evidence for it among oceanic populations would have important consequences for open-ocean zoogeography (eg McGowan, 1971; Badcock, 1981). It would tend to negate the apparent and unexplained distinction between broadly-distributed vs. restricted species. Division of broadly-distributed species into allopatric populations restricted to described faunal regions is consonant with the recognition of such regions based on concordantly restricted, rather narrow-ranging species. Such intraspecific populations may differ in aspects of their biology such as life history "strategy" (egg and larval size, fecundity, seasonality, etc.) reflecting differences in biological and/or physical parameters between regions (e.g. McGowan, 1971; Johnson & Barnett, 1975; Reid et al., 1978). The point is well made by Badcock (1981: 1488), ".....(while) the importance of recognizing distinct intra-specific populations and comprehending the nature of their differences can not be overstressed... intraspecific variation in most (mesopelagic) species is (very) poorly documented." To my knowledge Brinton's (1962: 178) classic demonstration of the "forms" of *Stylocheiron affine* is unparalleled by any mesopelagic fish study.

VINCIGUERRIA NIMBARIA: A CASE STUDY

Partly filling this gap (for fishes) is work in progress on variation in *Vinciguerria nimbaria* (Johnson & Feltes, 1984; and in prep.). There are at least four criteria to establish candidate species for study of polytypy: wide distribution (Fig. 1); apparent "eu-cosmopolitanism", sensu Table I; abundantly and synoptically represented in collections; and evidence of detectable and quantifiable inter-regional variation. *Vinciguerria nimbaria* was chosen for study because it fits well each criterion. *V. nimbaria*, exhibits demonstrable region to region variation in morphometric and meristic characters. Especially in gill raker counts there exists evidence of difference between equatorial vs.central populations (Fig. 2). Minimal criteria for establishment of polytypy for *V. nimbaria* (in the sense of the compound hypothesis advanced above) include:

1. evidence of consistent differences between specimens grouped by species-assemblage areas;
2. evidence that boundaries between "forms" (exact taxonomic status to be determined) are

Fig. 1 Distribution of samples of *Vinciguerria* included in this study. All specimens are *V. nimbaria* except those labelled RDS (= *V. mabahiss* Johnson & Feltes, 1984) and LUC (= *V. lucetia* Garman, 1899). Stippled bands denote areas transitional between water mass regions as depicted by Sverdrup et al. (1942). Solid lines (Atlantic only) indicate boundaries between regions recognized as mesopelagic faunal regions by Backus et al. (1977).
Atlantic areas include: CNA = subtropical North Atlantic (including Caribbean Sea and Gulf of Mexico); EQA = tropical Atlantic including Mauritanian Upwelling Region; CSA = subtropical South Atlantic.
Closed circles are *V. nimbaria* stations in central water mass regions (= "Central"). Open circles are *V. nimbaria* localities in equatorial water mass regions (= "Equatorial"), except Atlantic and South China Sea (see Johnson & Feltes 1984). Closed squares are *V. mabahiss* localities. Open squares are *V. lucetia* localities.


100W 80 60 40 20 0E 20 40 60 80 100 120 140 160 E 180 160 140 120 100 80 W
N 80 70 60 50 40 30 20 10 0 10 20 30 40 50 60 70 80 S
CNA
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TC1
TC2
TE
EQA
CSA
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PHS
NWG
CNP
EPW
CEP
EEP
LUC
CSP
SPOEL

concordant with boundaries between described species assemblage areas; note that "boundaries" are in fact transition zones that may vary from narrow and sharp (Johnson 1982: 225) to rather diffuse and broad (McGowan 1977: 425);

3. evidence that differences used in distinguishing "types" are not ecophenotypic in origin.

Material from two transects involving the crossing of known faunal boundaries, with *V. nimbaria* abundantly taken on each, has provided limited data relevant to these criteria.

The ANTIPODES transect (Johnson & Barnett, 1975) of August-September, 1970, offers limited support. *V. nimbaria* was taken at 19 stations in the Philippine Sea and at 6 stations in the South China Sea. A sharp model shift in photophore and vertebral counts and especially in gill raker counts (Johnson & Barnett 1975: Fig. 4, Tables 6,7,9) distinguishes specimens from the two areas while counts appear within-area homogeneous. The shift coincides geographically with a well-establshied faunal "boundary" separating equatorial (tropical) species (South China Sea) from central (subtropical) species (Philippine Sea) (e.g. compare the distribution of the euphausiid *Thysanopoda obtusifrons* with that of the Indo-Australian "forms" of *Stylocheiron affine* in Brinton, 1975). Overlap in character values and relative lack of South China Sea material preclude certain identification of specimens in the apparent zone of sympatry at stations 21 and 22 (Johnson & Barnett 1975)(fig. 4) - muddying the picture.

More convincing is newly-obtained evidence from the Atlantic. Specimens of *V. nimbaria* were studied from throughout the Nort Atlantic Subtropical Region (CNA, Fig. 1), most of the Atlantic Tropical Region (EQA) and 5 stations from the South Atlantic Subtropical Region (CSA) as drawn by Backus et al.(1977). In gill raker counts (Table II) there exists absolute difference, north and south central specimens have 17 to 21 gill rakers (total, first arch), equatorial specimens have 22 to 26. This difference applies throughout the CNA, EQA and CSA areas, satisfying the criterion of consistent difference between areas.

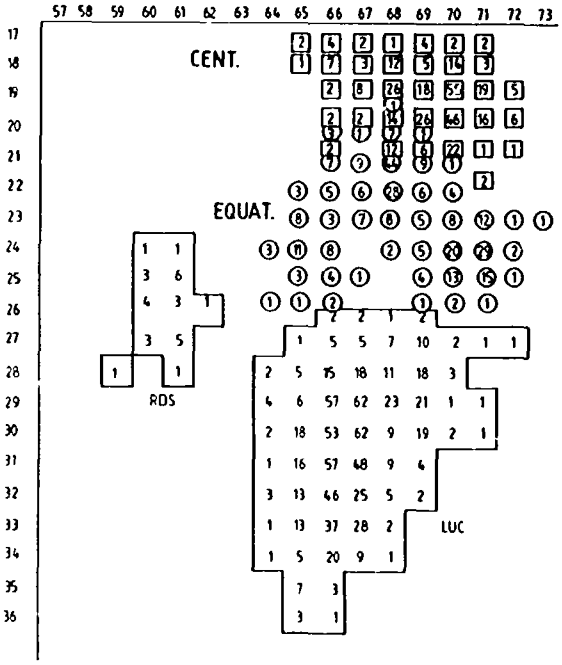

Fig. 2 Total body photophores tallied by gill raker numer (total on first gill arch) for specimens of *Vinciguerria*. Explanation of "Central" vs "Equatorial" given in legend to figure 1.

Substantial overlap occurs in all other examined characters although some hint of equatorial/central separation is suggested by principal components analysis of a 21 character morphometrics data matrix (Fig. 3).

In November, 1970, the Woods Hole vessel ATLANTIS II ran a double transect from central to equatorial and back into central. Three recognized Atlantic faunal regions (sensu Backus et al., 1977) were sampled (Fig. 4): the North Atlantic Subtropical Region (CNA: CNA6, TC1, TC2, CNA5), the Mauritanian Upwelling Region (MUR: TE) and the northeastern boundary region of the faunally-associated Atlantic Tropical Region (EQA:TE). On the southward leg (CNA6 to TC1 to TE) the shift between central vs. equatorial "types", as established by gill raker counts (Table 3), coincided exactly (Fig. 4) with the boundary between CNA and MUR, as drawn by Backus et al.(1977) Agreement was not as sharp on the northward leg, TE to TC2 to CNA5. At two stations, RHB 2076, RHB 2077, both "types" were taken

Table II Number of gill rakers (total, first arch) for Atlantic specimens of *Vinciguerria nimbaria*. Area designations keyed to figure 1.

		GILL RAKERS ON FIRST GILL ARCH													
Location	Nr.Stations	17	18	19	20	21	22	23	24	25	26	N	x	±	∂
CNA-1	(6)		3	20	7	2						32	19.25	.26	.718
CNA-2	(4)	2	3	3	1							9	18.33	.77	1.000
CNA-3	(10)		4	8	1							13	18.77	.36	.599
CNA-4	(4)		1	3	4							8	19.38	.62	.744
CNA-5	(6)	2	2	8	1							13	18.62	.53	.870
CNA-6	(5)			10	3							13	19.23	.26	439
CNA-7	(2)	2	6	15	7	1						31	18.97	.33	.912
CNA-8	(1)		2	8								10	18.80	.30	.422
CNA-9	(1)		1	8		1						10	19.10	.52	.738
TOTALS		6	22	83	24	4						139	18.99	.13	.789
TC-1	(9)	1	3	17	9	1						31	19.19	.29	.792
TC-2	(9)	9	23	43	9							84	18.62	.18	.820
TOTALS		10	26	60	18	1						115	18.77	.16	.849
TE	(23)						6	26	44	23	3	102	23.91	.18	.913
EQA-1	(1)							3	13	3	1	23	24.22	.32	.736
EQA-2	(1)							3	6	10	1	20	24.45	.39	.826
EQA-3	(1)							1	6	4		11	24.27	.43	.647
EQA-4	(1)							6	5	1		12	23.58	.42	.669
EQA-5	(1)							4	8	4	1	17	24.12	.44	.857
TOTALS							6	43	82	48	6	185	24.03	.13	.869
CSA-1	(1)		3	17	8							28	19.18	.24	.612
CSA-2	(1)			6	4							10	19.40	.36	.516
CSA-3,4,5	(3)	1	2	7	4							14	19.00	.51	.877
TOTALS		1	5	30	16							52	19.17	.19	.678

in the same net haul.

The fit of the equatorial "types" to MUR and EQA appears better in the north than in the east (Fig. 4) but this is also true for the MUR endemic myctophid, *Lampadena pontifex* (Nafpaktitis et al., 1977: Fig. 120). It most likely reflects the seasonal hydrographic variability of MUR, known to be greater in the south MUR (Wooster et al., 1976; Badcock, 1981). A plot of ATLANTIS II records for *V. nimbaria* against temperature at 200m (Fig. 5) demonstrates the association of the equatorial "type" with cooler MUR water.

Accumulating faunal evidence (Krefft, 1974; Backus et al., 1977; Badcock, 1981; Johnson, 1982) has established the CNA, EQA and CSA as comparable to species-assemblages areas (ecosystems of McGowan, 1977) in the Pacific. The status of MUR is unusual, for, as noted by Badcock (1981: 1485), it is the only North Atlantic region inhabited by species with northern (sensu

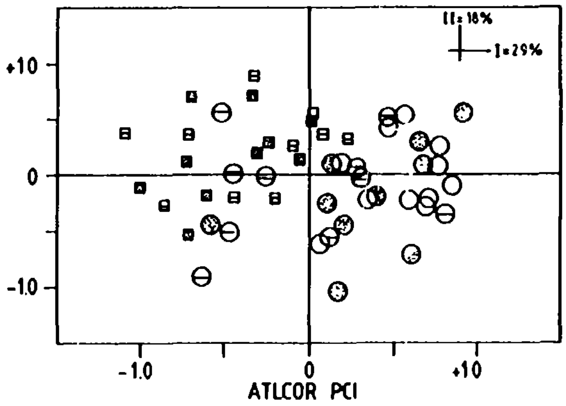

Fig. 3 Relative position of 51 specimens of *Vinciguerria nimbaria* in the projection of the first two principal components of a 21-morphometric character correlation matrix (characters used expressed as proportions of standard length; characters and methods as in Johnson & Feltes, 1984). Squares= equatorial specimens. Circles= central specimens.

Table III Number of gill rakers (total, first arch) for specimens of *Vinciguerria nimbaria* from ATLANTIS II, cruise 59, November, 1970.

TOTAL GILL RAKERS ON FIRST GILL ARCH												
	17	18	19	20	21	22	23	24	25	26	TOTAL	MEAN ±
2021			8	3							C* 11	19.27± 0.31
2024,2025	1		3	2	1						C 7	19.29± 1.16
2028,2029,2030		1	6	1							C 8	19.00± 0.45
2034,2035		2	8	6							C 16	19.25± 0.36
2037,2044,2047							2	2	1		E 5	23.80± 1.04
2048,2049,2050						1	6	5	2		E 14	23.57± 0.49
2051						4	4	12	3	1	E 24	23.71± 0.44
2056,2057,2058,2059							3	7	3		E 13	24.00± 0.43
2060,2062							1	4	7		E 12	24.50± 0.43
2065,2066,2070							3	5	3		E 11	24.00± 0.52
2071,2073						1	3	7	3		E 14	23.86± 0.50
2075							2	1	1	1	E 5	24.20± 1.62
2076	2	3	7	4			2				C16 E 2	18.81± 0.52
2077	1	6	7	1				1		1	C 15 E 2	18.53± 0.41
2080,2081	3	6	2	1							C 12	18.08± 0.57
2082,2083,2084	3	7	20	1							C 31	18.61± 0.26
2085		1	7	2							C 10	10.10± 0.41
2088	1		4	1							C 6	18.83± 1.03
CENTRAL TOTALS	11	26	72	22	1						132	
EQUATORIAL TOTALS						6	26	44	23	3	102	

* Station positions given in Fig. 4 (C= Central, E= Equatorial).

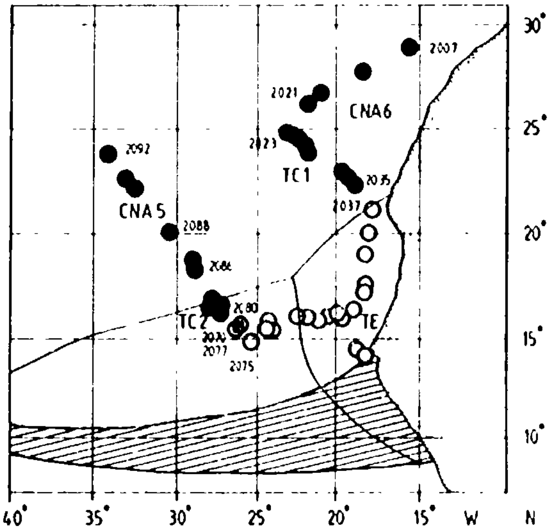

Fig 4 Distribution of samples of *Vinciguerria nimbaria* taken by the ATLANTIS II, Cruise 59, November, 1970. Four digit numbers are Richard H.Backus (RHB) station numbers (Woods Hole Oceanographic Institution). Area designations as in figure 1. The wide stippled band indicates the zone of transition between the North Atlantic and South Atlantic Central Water Mass Region as depicted by Sverdrup et al.(1942). The solid lines indicate the boundary between the North Atlantic Subtropical Region, Mauritanian Upwelling Region and Atlantic Tropical Region as depicted by Backus et al. (1977). Closed circles = "Central" specimens; open circles indicate "Equatorial" specimens. The partly closed circles indicate the two stations where both "types" were captured in the same haul. See text for explanation.

Backus et al., 1977), subtropical and tropical distribution patterns. For *V. nimbaria* as for the pair *Coccorella atlantica* vs. *Scopelarchus guentheri* (Johnson 1982: Fig 54) MUR is faunally associated with EQA. Thus the available data show that *V. nimbaria* satisfies the criteria of difference and boundary concordance.

Evidence for the criterion of genetic distinction is, as usual, limited. gill raker counts (Table II) are homogeneous throughout the quite large CNA vs EQA vs CSA areas, but shift dramatically (Table III) at the boundaries crossed by the ATLANTIS II transect; the material examined from CNA was collected throughout the yearly cycle; and the ATLANTIS II transect material for both CNA and EQA+MUR contained specimens from throughout the size-frequency spectrum.

CONCLUSIONS

I conclude that in the Atlantic, at least, *Vinciguerria nimbaria* is polytypic and surmise that this is true throughout its range. I predict that additional study will show this to be a more general condition among mesopelagics than now known, whatever the taxonomic status of the "types" recognized (see Gibbs, this volume), to the extent that this prediction is true, will the apparent disparity between broadly-distributed and narrowly-restricted open ocean midwater species diminish.

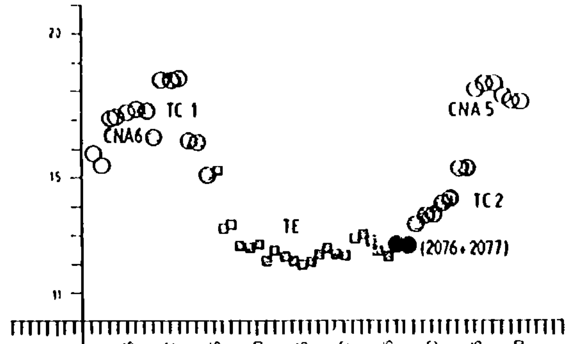

Fig.5 Plot of temperature at 200m by "type" of *Vinciguerria nimbaria* taken during Cruise 59 of the ATLANTIS II while occupying the stations depicted in figure 4. Circles = "Central", squares= "Equatorial", closed circles indicate the two stations (2076+2077) where both "types" were taken in the same net haul.

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BIOGEOGRAPHY OF THE HUMPBACK WHALE, MEGAPTERA NOVAEANGLIAE, IN THE NORTH ATLANTIC

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INTRODUCTION

Current studies on the humpback whale *Megaptera novaeangliae* offer insights into baleen whale biogeography and show great contrasts to the other organisms treated in this symposium. Each of the approximately 5500 humpback whales (Balcomb et al., 1985) in the North Atlantic Ocean commands, on average, about 54,000km^3 of water and 13,740km^2 of ocean surface. Each individual is large (up to 19m long), potentially long-lived (up to 50 years or more), fast (up to 10 knots) and able to swim through the various water masses of an entire ocean basin. Large size, long lifetimes and large potential ranges buffer individuals and the population from seasonal and other short-term environmental changes. Considering such capabilities, what factors limit the distribution of this species and other baleen whales ?

THE HUMPBACK

Tracking whales individually-identified by photographs of distinctive markings, has revolutionized study of their distribution and ecology. All individuals are potentially recognizable by this relatively inexpensive, benign (Payne, 1983) technique . Humpbacks are distinguished by individual variations in the black and white pattern of the ventral side of the flukes (Katona & Whitehead, 1981). Population size can be estimated by applying mark-recapture techniques (Seber, 1972; Balcomb et al., 1985) to the photographic collection.

As do nearly all baleen whales, humpbacks migrate annually between productive high latitude summer feeding ranges, mainly on or along continental shelves, and lower latitude winter breeding ranges. Their flexible diet includes schooling fish (herring, *Clupea harengus*; capelin, *Mallotus villosus*; and sand lance, *Ammodytes americanus* in the North Atlantic) plus krill, especially *Meganyctiphanes norvegica*. Prey type, abundance and distribution influence local feeding behaviour (Hain et al.,1982; Baker & Herman 1985) and distribution on the summer range. For example, short term and year-to-year changes in Newfoundland humpback distribution are related to changes in capelin abundance and distribution (Whitehead & Carscadden, 1985), but many individuals remain throughout the summer at Stellwagen Bank, Massachusetts, to feed upon a resident population of sand lance currently in high abundance (Mayo, 1982). Fine-scale distribution is also affected by the whales' ability to recognize individuals and respond to them differentially. Some humpbacks have been seen together over much of a feeding season, and occasionally during several feeding seasons (Baker & Herman, 1985; Weinrich, 1983; D.Matilla, pers. comm.). Factors underlying such associations could be as mundane as similar sizes, swimming speeds, diving capabilities, or physiological states, but kinship could also be involved.

Humpbacks do not eat during winter while gathered to calve and mate within 20 degrees of the equator in clear, poorly-productive, shallow, warm water (about 25°C) at banks or bays protected from heavy surf by coral reefs or other geologic features. Large whales may occasionally overwinter in cold water, but the 5m long newborn calves are born in the warmest waters known to be used for breeding by any baleen whale. Perhaps the long flippers, each about one third of the body in length, would in colder water drain heat from the thin newborn at an intolerable rate. Later in life the flippers will be used to manoeuver, herd fish, guide calves, pound aggressively on the water or on other whales, possibly clasp a partner during mating (not yet observed) and, ironically, to dump excess heat while in warm waters (Brodie, 1975). Concentration of female humpbacks at traditional calving sites attracts males for mating. "Rowdy" groups of males vie for dominance, competing physically and with sound for access to females (Tyack & Whitehead, 1983; Baker & Herman, 1984). Males may select smooth bottom topography to optimize sound propagation (Whitehead & Moore, 1982).

Analysis of photographs of over 3500 individual humpbacks from the North Atlantic (Table I) and over 900 resightings of identified individuals (Table II) reveal that this population comprises at least four, and probably five, separate feeding substocks (Iceland-Denmark strait; western Greenland; Newfoundland-Labrador; Gulf of St. Lawrence; and Gulf of Maine - Nova Scotia) to which high percentages of individuals return annually (Table III). No interchange has yet been observed between the first three units and only one whale has been seen in both Newfoundland and the Gulf of Maine. Less clear is the situation in the Gulf of St. Lawrence. Some humpbacks return there annually (Table III), but ten whales have been seen in both the Gulf of St.Lawrence and in Newfoundland; and nine different whales have recently been seen in both the Gulf of St.Lawrence and the Gulf of Maine.

Table I Distribution of photographs of humpback whale flukes contained in Atlantic Humpback Whale Catalogue as of May 15, 1985.

EUROPE	**10**
NE ATLANT	**0**
ICELAND	**18**
GREENLAND	**149**
NFLD/LAB	**1413**
G.ST.LAWR	**97**
GOM/N.S	**340**
U.S.COAST	**3**
BERMUDA	**73**
SILVER BK	**976**
PRTO.RICO	**474**
VIRGINS	**10**
total	**3563**

Table II also shows that individuals from all five of the feeding substocks migrate to the Antilles during winter for breeding (Katona et al., 1985a). Chi-square analysis shows that a constant proportion of whales from each of the five northern regions visits the winter range

Table II Geographical distribution of resightings of individually-identified humpback whales from the North Atlantic. Within-region resightings are for intervals of one year or longer.

	I	**G**	**N**	**L**	**M**	**U**	**B**	**S**	**P**	**V**	**A**	**E**
ICELAND	0	-	-	-	-	-	-	-	-	-	-	-
GREENLAND	0	43	-	-	-	-	-	-	-	-	-	-
NFLD/LAB	0	0	205	-	-	-	-	-	-	-	-	-
G.ST.LAWR.	0	0	10	20	-	-	-	-	-	-	-	-
GOM/NS	0	0	11	9	201	-	-	-	-	-	-	-
E.COAST,U.S.	0	0	0	0	1	0	-	-	-	-	-	-
BERMUDA	0	2	10	1	7	1	1	-	-	-	-	-
SILVER BK	1	15	142	7	25	0	8	40	-	-	-	-
PTO.RICO	3	1	63	11	15	0	3	40	24	-	-	-
VIRGIN IS.	0	1	0	0	0	0	0	0	1	0	-	-
N.ATLANTIC	0	0	0	0	0	0	0	0	0	0	0	-
EUROPE	0	0	0	0	0	0	0	0	0	0	0	0

Table III Within-region year-to-year resightings of individually-identified humpback whales.

Location	Returns	Total No.	Percentage
ICELAND	0	18	0.00
GREENLAND	43	149	28.86
NFLD/LAB	205	1413	14.51
G.ST.LAWR	20	97	20.62
GOM/N.S.	201	340	59.12
BERMUDA	1	73	1.37
SILVER BK	40	976	4.10
PRTO.RICO	24	474	5.06

(Silver Bank, Puerto Rico, Virgin Islands and further south) and also the major breeding location, Silver Bank, which may now host up to 85% of western North Atlantic breeding humpbacks (Winn et al., 1975). However, whales from both Iceland and the Gulf of St.Lawrence appeared to be significantly over-represented at Puerto Rico. Further studies on the Antillean breeding range are needed to discover whether whales from the different feeding substocks or individuals of different ages or classes use different portions of the habitat. Starting in late March, humpbacks migrate north, passing Bermuda (Table II). Sighting of an Iceland whale at Bermuda during April, 1985 (G.Stone & S.Katona, unpubl. data), shows that some whales from each feeding substock migrate past that island.

Payne & Katona (1985) presented evidence to suggest that each ocean basin, including the North Atlantic, is inhabited by one genetic stock of humpbacks. This appears true for the western North Atlantic, at least, where out of eight "rowdy groups" observed at Silver Bank that contained two or more whales known from the northern range, six contained individuals from two different feeding substocks (Katona et al., 1985b). Additional photography of humpbacks from the eastern North Atlantic is needed in order to discover whether those whales breed in the western North Atlantic (Christensen, 1984) or at some location in the eastern sector, such as the Cape Verde Islands.

Long term observations should reveal whether currently depleted or abandoned portions of the historical range (Mitchell & Reeves, 1983) can be recolonized. Factors such as preemption by human activities; overall population trend; habits of site-fidelity displayed by individuals; extirpation of groups making traditional use of particular locations; and transmission of information about migration paths from mother to calf will certainly be involved.

BRIEF BIOGEOGRAPHICAL COMMENTS ON OTHER BALEEN WHALES

Ten species of Mysticeti exist. All six members of the family Balaenopteridae (*Balaenoptera musculus*, blue; *B. physalus*, finback; *B. borealis*, sei; *B. edeni*, Bryde's; *B. acutorostrata*, minke; plus *Megaptera novaeangliae*, the humpback whale) inhabit the North Atlantic, North Pacific and Southern Ocean. Each ocean basin probably contains a separate population of each species. Inter-ocean gene flow must be high enough to prevent speciation, but low enough to promote sub-specific morphological differences within nearly all species. The Balaenopteridae may have originated from Miocene Cetotheres (Barnes et al., 1985), evolving and radiating in warm waters of the North Atlantic, probably in the Middle Miocene, then crossing the equator to the Southern Ocean and the Central American seaway to the North Pacific (Gaskin, 1982: 238). All species but *B. edeni* responded favorably to climatic cooling and extended their ranges to high latitudes. None of the species in the genus *Balaenoptera* are known to aggregate for mating or calving. The low frequency calls of blues, finbacks and minkes, at least, potentially carry for great distances and would be suitable for communication between individuals scattered on a breeding range (Payne & Webb, 1971).

Distribution is restricted for the other three species. The gray whale (*Eschrichtius robustus*), the monotypic representative of the family Eschrichtidae), is unique in several respects. Its fossil history can only be traced back to the late Pleistocene (Barnes et al., 1985). Living gray whales are known only from the North

Pacific. The presence of sub-fossil Atlantic remains (Mead & Mitchell, 1984) and the lack of pre-Pleistocene fossils in California suggest colonization from the Atlantic via the Arctic Ocean during the last warm period (Gaskin, 1982: 238). No record of the species exists from the Southern Ocean. The gray whale's annual 4000 mile journeys between Bering Sea feeding grounds and Baja California breeding lagoons are the longest known for any mammal. It is the only baleen whale known to feed primarily by sucking up benthic infauna (Nerini & Oliver, 1983), a feature that may limit it largely to soft, shallow, productive feeding locations.

The family Balaenidae, the oldest of the modern mysticete families (Lipps & Mitchell, 1976), displays a curious mixture of biogeographical distributions. The right whale (*Eubalaena glacialis*) is distributed in the balaenopterid pattern, and is the only species besides gray whales and humpbacks known to aggregate for breeding in coastal waters (Payne, 1976). The bowhead (*Balaena mysticetus*) is Arctic and circumpolar, with no known Southern Ocean remains. But the poorly known pygmy right whale (*Caperea marginata*), is circumpolar in cold-temperate waters (5° to 20°C) through out the Southern Ocean, with no known northern remains. Some authors give this species family status as Neobalaenidae (Barnes et al., 1985). Balaenids are specialized to eat small zooplankton at the surface, at depth, and sometimes at the bottom. Right whales and bowheads require patches of high productivity to survive (Kenney et al., in the press) and these species may be tied more closely to productivity-enhancing oceanographic features than is the case for fish-eating baleen whales.

Strong ecological and morphological differences separate the three living families of mysticetes. The three balaenids feed in similar fashions, but are separated geographically. The six balaenopterids are not so clearly separated, but ecological and geographical differences do exist. As summarized by Nemoto (1971) and Pivorunas (1979) the blue specializes on krill, and the others feed with varying flexibility or preference on fish, krill, copepods and occasionally squid. Several species may feed in the same general area, sometimes with whales from another family, but the different species feed in different manners (Watkins & Schevill, 1979) except perhaps in the Antarctic when all feed on krill. Actual mixed-species groups are rare. Appreciable interspecific separation, as well as intraspecific separation of different sizes or classes of individuals, have been observed in the southern ocean (Laws, 1985) and whaling-related changes in pregnancy rate and age of first reproduction for some species suggest decreased competition for krill. Mitchell (1974) hypothesized that competition by sei whale's for copepods may limit the recovery rate of North Atlantic right whale populations, but fish, basking sharks and some invertebrates could be equally strong competitors. Recent studies using individual photo-identification suggests that minke whales (Dorsey, 1983) , blue whales (R. Sears, pers. comm.) and finback whales (M. Pratt, pers. comm.) return annually to habitual feeding areas. Some of the minke whales studied by Dorsey (1983) apparently patrolled home ranges. So far no evidence exists for interference-type competition.

CONCLUDING REMARKS

The first cetaceans (Archaeoceti) appear to have evolved from a group of early Eocene condylarths (family Mesonychidae) that gradually invaded shallow productive bays of the eastern Tethys Sea to feed on fishes (Gingerich et al., 1983; Barnes & Mitchell, 1978)). By the middle Oligocene the Mysticeti mode of feeding was already fully evolved and the group was probably present in all oceans (Whitmore & Sanders, 1976). Radiation of both Odontoceti and Mysticeti occured in the Miocene, by which time both groups were fully adapted to aquatic life (Whitmore & Sanders, 1976), and may have occured in response to increased ocean productivity stimulated by increased upwelling (Lipps & Mitchell, 1976).

Early mysticetes must have crossed the Equator during dispersal, but modern mysticetes apparently do not. Behavioural traits, rather than physiological ability, may prevent modern mysticetes from crossing hemispheres. Many aspects of mysticete behaviour, including migration, seem to reflect ancestral affinity with ungulates. Mysticete ancestors were probably sufficiently large and powerful to avoid random dispersal by storms or currents. If early ancestors showed group cohesion and fidelity to feeding and breeding sites, it is not likely that Equator-like "barriers" would have been crossed any more readily than they are today, suggesting that dispersal must have occured along favourable paths. If so, detailed paleoecologic knowledge of surface waters would shed light on early dispersals and radiations. Knowledge of early dispersal patterns would help explain major evolutionary divergences at the family level. A series of isolating mechanisms is needed to explain evolution of the balaenopterid species flock if all six species arose in the North Atlantic. Possible factors could include the behavioural balance between site-fidelity, home ranging and migratory straying; range expansions and contractions related to warming or ice formation; expansion and contraction of upwelling systems; and inter-species competition at easily accessible productive sites.

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ONTOGENETIC VERTICAL MIGRATION PATTERNS OF PELAGIC SHRIMPS IN THE OCEAN; SOME EXAMPLES

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INTRODUCTION

In many pelagic shrimps, the larvae, juveniles, and adults are separated vertically and horizontally. For example, the principal larval population of a sergestid, *Sergestes similis,* always occurs between 30 and 80m depth both day and night off southern California, but adults extend to depths of 50 to 600m, through extensive diel vertical migration (Omori & Gluck, 1979). Horizontal distribution is largely affected by the ontogenetic migration. The total adult distribution is often much broader than the reproductive (viable) range (e.g. *Calanus cristatus,* Omori, 1967). The picture of biogeography for a species significantly changes depending on what developmental stage is studied.

Omori (1974) reviewed ontogenetic migration of pelagic shrimps and concluded that there are three distributional types, as follows:

1. Species usually living in the epipelagic and upper mesopelagic zones and discharging their eggs in the euphotic zone where larvae hatch and remain initially. The amplitude of diel vertical migration increases with growth.
2. Species living in the lower meso- and bathypelagic zones. Their spawning or hatching takes place in the uppermost part of the vertical range of adult females; the eggs or larvae move upward to the euphotic zone. The juveniles and adolescents gradually move into deeper water.
3. Species whose spawning, larval and adult life take place in the bathypelagic zone. No stages occur in the surface or sub-surface zone.

In order to verify this conclusion, and to evaluate significance of ontogenetic migration, relationships between vertical distribution and growth of a number of shrimps were analyzed from samples obtained in the northwestern Pacific off Japan. The sampling method was not the best for the purpose of the present investigation, as the mesh size (5.6mm) was too coarse to sample larvae and small immatures. Although the analysis was thus restricted to juveniles and adults, the results provide information concerning ontogenetic migration and vertical distribution.

METHODS

Sampling methods have been described in our previous report (Kikuchi & Omori, 1985). Pelagic shrimps were collected at Station B (30°00'N, 147°00'E; sounding ca. 6200m) during a cruise aboard the R/V Kaiyo-Maru from June 1 to 25, 1982. Discrete horizontal sampling was carried out using the KOC sampler with 5.6mm in mesh size (Anonymous, 1980) at night or daytime, avoiding twilight hours. In all, 28 tows were made from 17 layers between 150 and 6100m depths. The shrimps were sorted, identified and counted immediately after being caught. The carapace length (CL) from the post-orbital margin to the median posterior edge of the carapace, was measured to the nearest 0.5mm in all specimens, except in five species which were either small in size or numbers.

RESULTS AND DISCUSSION

Among the 17,440 individuals collected, 57 species, representing seven genera of Penaeidea and twelve genera of Caridea, were identified. *Acanthephyra quadrispinosa* and *Sergia prehensilis* were the most abundant species and comprised 34.2% and 12.9% respectively of the

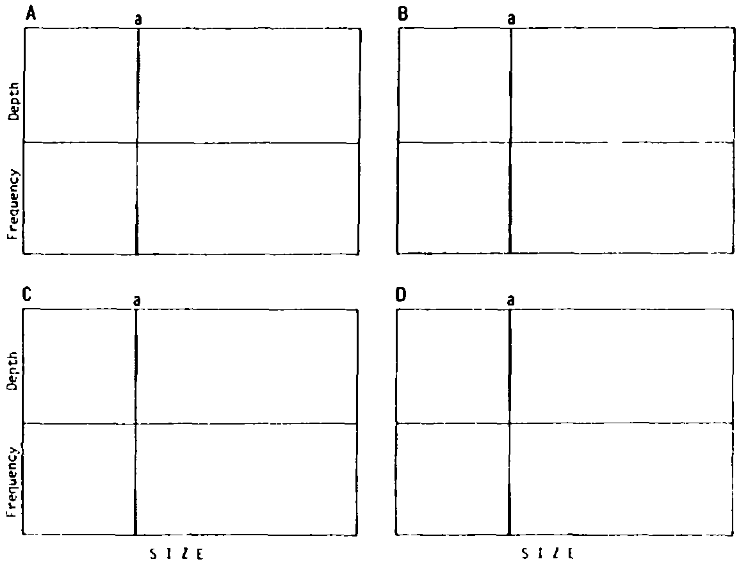

Fig. 1 Schematic illustration of four types of ontogenetic vertical migration of pelagic shrimp.

total number of specimens. Fourteen other species contributed between 7.9 and 1.0%. Pelagic shrimps could be divided into the following 5 types according to their adult diel migration patterns (Kikuchi & Omori, 1985):

1. Vertical migrants living mainly in the upper mesopelagic zone;
2. Extensive diel vertical migrants living in a wide range of the mesopelagic zone;
3. Vertical migrants living in the lower mesopelagic zone;
4. Non- or slight diel migrants of which the principal population lives in the upper bathypelagic zone by both night and day;
5. Non-migrants living in the lower bathy- and abyssopelagic zones. (Table I).

Relationships between vertical distribution and growth of twenty species showed existence of four patterns of life history and ontogenetic migration (Fig. 1; Table I). Based on the general body shape of pelagic shrimps and size frequency distribution of the catch, we found that all individuals smaller than 8.0mm CL were not quantitatively collected in the present sampling. Line "a" in figure 1 means 8.0mm CL, and in data interpretation we have assumed that shrimps smaller than line "a" were undersampled.

Type A - The amplitude of diel vertical migration increases and the shrimps gradually shift to greater daytime depths with increasing size. The size frequency histogram consists of a single mode (one year class).

Type B - Adults occur in deeper water than larvae and juveniles. The size frequency histogram consists of two or more modes. Diel vertical migration is limited or non-existent.

Type C - Ontogenetic vertical migration similar to Type A, but the size frequency histogram consists of two or more modes, indicating a life span of two years or more.

Type D - Larvae and adults live at the same depth. Size frequency histogram with two or more modes.

In the present study, all species of type A were smaller than 17mm CL. Their larvae and juveniles are smaller than 8mm CL. These species are mainly epi- and upper mesopelagic sergestids and penaeids such as *Sergestes armatus* and *Sergia scintillans* (Fig. 2). Their life span is 1.0 to 1.5 years as shown in *Sergestes similis* and *Sergia lucens* (Omori, 1969; Omori & Gluck, 1979). The amplitude of the adult's diel vertical migration covers the greater part of the vertical range of their ontogenetic migration. Spawning and/or hatching takes place in the upper layers and larvae feed in the euphotic zone.

Type B represents the pattern of typical lower

Table I The characteristics in vertical distribution of pelagic shrimps.

Species:	Relative abundance in total number of species (%)	Minimum size (CL) of the adult female (mm)	Diel vertical migration pattern (Type)	Ontogenetic migration pattern (Type)
Sergestes armatus	5.4	8.1	2	A
Sergestes sargassi	2.1	6.6	1	A
Sergestes seminudus	1.7	11.4	1	A
Sergia japonica	4.2	11.1	4	C
Sergia laminata	2.5	7.6	3	A
Sergia prehensilis	12.9	8.1	1	A
Sergia scintillans	1.9	7.5	1	A
Gennadas incertus	6.7	n.d.	2	A
Gennadas parvus	2.5	n.d.	3	A
Gennadas propinquus	7.9	n.d.	2	A
Bentheogennema borealis	0.8	12.4	4	C
Bentheogennema intermedia	+	n.d.	4	B
Oplophorus spinosus	2.1	13.8	1	C
Acanthephyra quadrispinosa	34.2	15.8	3	D
Notostomus japonicus	+	n.d.	3	C
Systellaspis debilis	0.4	11.0	1	C
Hymenodora frontalis	2.5	9.1	4	C
Hymenodora glacialis	1.3	13.7	5	B
Hymenodora gracilis	2.1	8.4	5	C
Parapasiphae sulcatifrons	0.8	19.0	4	C
Parapandalus richardi	6.3	9.1	1	n.d.

+ = relative abundance < 0.3%; n.d.= not determined

meso- and bathypelagic species. To explain this pattern, there seem to be two possibilities, e.g. eggs float to the upper layers of their vertical range before hatching, or hatching occurs in the deep layer and larvae move to the upper layers. Although movement of eggs or larvae towards shallow layers has not been confirmed in the present study, we consider the species such as *Hymenodora glacialis* which perform non- or limited diel vertical migrations have this pattern (Fig. 2). Vinogradov (1968) reported this type of ontogenetic vertical migration in *Hymenodora frontalis* and *H. glacialis* in the Kurile-Kamchatka Trench. A similar pattern of migration is shown in a number of other pelagic organisms such as the euphausiids, *Thysanopoda egregia* (Brinton, 1962), and four gonostomatid species of the genus *Cyclothone* (Badcock & Merrett, 1976).

Type C includes both diel vertical migrant, such as *Oplophorus spinosus*, and non- or slight diel migrant such as *Bentheogennema borealis* (Fig. 2). These species increase their range of vertical distribution with increasing body size and presumably locomotive power.

Notostomus japonicus is tentatively included in type C (Fig. 2), but questions about its growth need to be resolved to define its life history. Although Krygier & Pearcy (1981) reported the presence of an intermediate size class, 24-29mm CL from off the Oregon coast, the present size frequency histogram shows only two

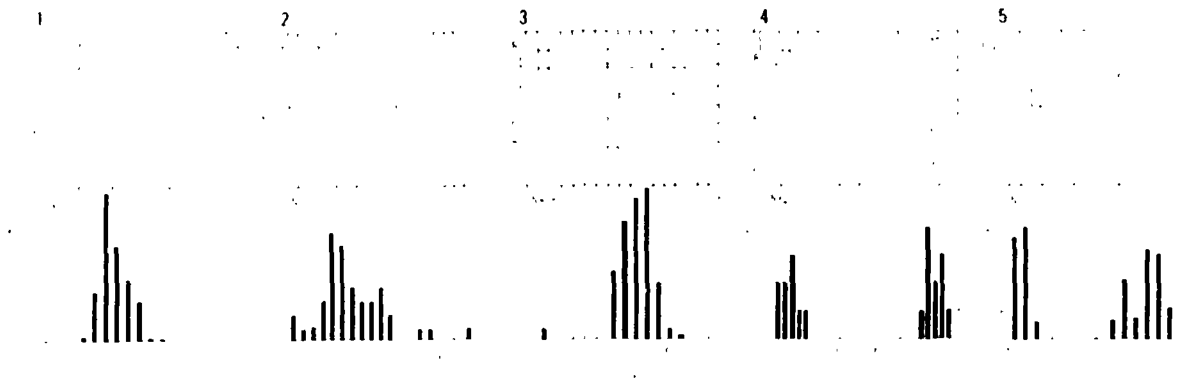

Fig. 2 Vertical distribution and size frequency histograms of five pelagic shrimp species at station B. Broken horizontal bar - daytime distribution, solid bar - night distribution. 1. *Sergestes armatus* (ontogenetic migration type A); 2. *Hymenodora glacialis* (type B); 3. *Bentheogennema borealis* (type C); 4. *Notostomus japonicus* (type C); 5. *Acanthephyra quadrispinosa* (type D).

classes, i.e. immatures of 5-10mm CL and adults of >40mm CL, with a large separation between them. This suggests that the former class is able to grow to the latter size within one year, which is much faster than the generally accepted estimates of growth rates for mesopelagic and bathypelagic species (see Mauchline, 1972).

Type D is represented by *Acanthephyra quadrispinosa* (Fig. 2). This species spawns from April to November, hatches from December to May, and grows to 6mm CL within one year and to 15-18mm CL (adults) within two years of age (Aizawa, 1974). The specimens in the present sample are mainly of one year class. Because 0-year class are less than 5mm CL, the range of their vertical distribution could not be clarified.

CONCLUSION

The present analysis indicates no apparent association between diel migration pattern and life history/ontogenetic migration pattern. It means that, although many species have broadly overlapping depth ranges, each has a different adaptation and biological strategy in relation to depth distribution. Within depths of co-occurrence of species, the difference of size between species is considerable, suggesting that differences in feeding habits and seasonal variations in abundance permit their co-occurrence.

In general, the size frequency histogram of epi- and upper mesopelagic species consists of one to two clear modes, indicating that their spawning and/or hatching is seasonal, growth is rapid, and life span is comparatively short. In contrast the size frequency distribution of lower meso- and bathypelagic species is often composed of a number of unclear modes. This phenomenon can be explained by the trend in the less variable environment for reproduction to occur whenever circumstances become favourable, growth is slow, and longevity considerable.

The present four types must be the only examples among many more different ontogenetic migration patterns. In fact, some species of the Oplophoridae produce relatively few large yolky eggs and others carry a large number of small eggs (Omori, 1974), and as in the case of the type C, both diel and non-diel migrants are dealt with in the same group. Even in the bathypelagic species in the type B, some may spend the larval stage in the epipelagic zone but others may stay in the meso- or bathypelagic zone. These species having different life strategies and behaviour would have been different in ontogenetic patterns which need to be defined as more data become available.

Larval vertical distribution may be determined by the pattern of depth distribution and migration of the adults; by the type of embryonic development; and by the relative amount of yolk present in the embryo at the time of hatching (Ziemann, 1975). Further studies are needed on the vertical distribution of eggs and larvae, and hence, more detailed taxonomic studies of developmental stages are necessary.

Clarification of the ontogenetic migration patterns will allow determination of its biological meaning and function, and therefore, of the relationship between physical process and pelagic biogeography and of evolutionary relationship between food competition/predation and ontogenetic migration.

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IMPORTANT OF VERTICAL DISTRIBUTION STUDIES IN BIOGEOGRAPHIC UNDERSTANDING : EASTERN TROPICAL PACIFIC VS. NORTH PACIFIC CENTRAL GYRE ICHTHYOPLANKTON ASSEMBLAGES

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INTRODUCTION

Biogeographic studies of mesopelagic fishes traditionally have been based on distributions of juvenile and adult stages relative to large scale hydrographic and biological features (e.g., water masses and productivity levels). Enhanced understanding of factors possibly affecting the composition and structure of fish assemblages within different zoogeographic regions might result from an examination of both larval and adult stages relative to finer scale distributions of physical and biological conditions. As an example are the results of a comparative study of 0-100m ichthyoplankton assemblages sampled by replicated 25m depth stratified bongo tows at 28°N 155°W in the North Pacific central gyre (CG) and near 13°N and 130°W in the Eastern Tropical Pacific (ETP) during late summer (Loeb & Nichols, 1984).

RESULTS

Doubled estimated abundance and lower diversity of ETP vs CG ichthyoplankton (Table I) can be related to overall higher primary productivity and hydrographic complexity and variability of the ETP ecosystem relative to the CG. Despite similar mixed layer temperatures and depths (ca. 26°C, 40m) the assemblages had significantly different (Kolmogorov-Smirnov test, P<0.01) vertical distribution patterns (Fig. 1): 70% of 0-100m CG larvae occurred within the upper 50m (mixed layer), while 66% of ETP larvae were below this layer.

The overall depth distribution differences of ETP and CG larvae have associated species composition differences. Gonostomatids and myctophids contributed >90% of total larvae in the two areas, however, both families had significantly deeper distributions in the ETP than

Table I. Comparisons of ichthyoplankton collected in nighttime stratified bongo samples in the North Pacific central gyre and eastern tropical Pacific during late summer. Mixed layer temperature (ca. 26°C) and depth (ca. 40m) was similar in both cases.

	CENTRAL GYRE			EASTERN TROPICAL PACIFIC		
DEPTH INTERVAL	**MEAN NO. 1000m-3**	**NO. TAXA**	**NO. SAMPLES**	**MEAN NO. 1000m-3**	**NO. TAXA**	**NO. SAMPLES**
0-25m	**312**	**41**	**(10)**	**242**	**28**	**(15)**
25-50m	**676**	**60**	**(10)**	**642**	**32**	**(13)**
50-75m	**254**	**49**	**(10)**	**1034**	**35**	**(14)**
75-100m	**166**	**50**	**(10)**	**777**	**38**	**(14)**
TOTAL	**1408**	**83**	**(40)**	**2695**	**56**	**(56)**

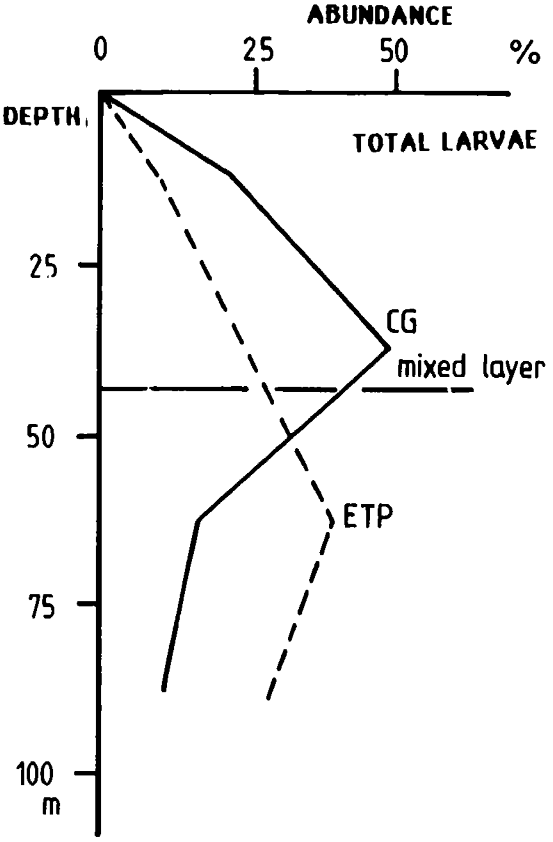

Fig. 1 Nighttime vertical distribution profiles for ichthyoplankton in the North Pacific central gyre (CG) and Eastern Tropical Pacific (ETP) during late summer. Distribitions represented as percentage of total 0-100m abundance present within each of four 25m depth intervals.

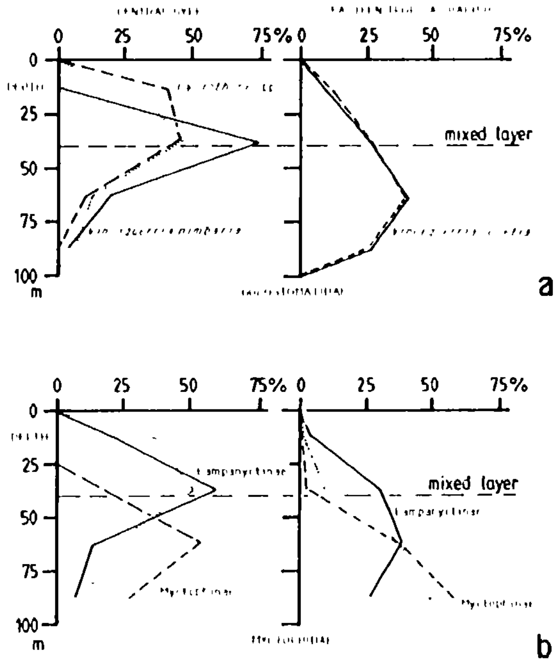

Fig. 2 Nighttime vertical distribution profiles for major ichthyoplankton components in the North Pacific central gyre and Eastern Tropical Pacific during late summer. Distributions are based on percentage of total 0-100m abundance present within each of four 25m depth intervals and are presented for (a) total gonostomatids (dotted line) and numerically dominant gonostomatids species and (b) total myctophids (dotted line) and myctophid subfamilies Lampanyctinae and Myctophinae.

CG (Fig. 2; Kolmogorov-Smirnov tests, P<0.01 in both cases). Dominant central gyre gonostomatids *Cyclothone* spp. (27% of total larvae) and *Vinciquerria nimbaria* (9%) had maximum abundances at 25-50m. In the ETP shallow living *Cyclothone* spp. larvae were rare (<1% of total); dominant *Vinciguerria lucetia* (77%) had maximum abundance at 50-75m and was significantly deeper (P<0.01) than its central gyre congener. In both areas larvae of myctophid subfamily Lampanyctinae occurred significantly shallower (P<0.01) than those of subfamily Myctophinae. In the CG larval lampanyctines outnumbered myctophines by 4:1; in the ETP larval myctophines outnumbered lampanyctiness by 4:1. Additionally, both subfamilies had significantly deeper distributions in the ETP than CG (P<0.05 in both cases; Fig. 2).

The larval composition and vertical distribution differences between the CG and ETP are associated with different migratory habits of the dominant adult populations. *Cyclothone* spp., the central gyre dominants, are non-migrators; *Vinciquerria lucetia*, the ETP dominant, migrates into the upper 100m at night (Robison, 1973). In the central gyre, myctophine adults generally migrate to the surface or the mixed layer, while lampanyctine adults generally have nighttime distributions below the mixed layer (Clarke, 1973; Loeb, 1980)(Fig. 3). In the ETP, adults of six of the seven myctophine species and two of the four lampanyctine species represented in the ichthyoplankton migrate to the surface (neuston) layer at night to feed (Robison, 1973; Wisner, 1976; Loeb & Nichols, 1984)(Fig 4).

These distributional, compositional and behavioral differences reflect fundamental differences between environmental conditions affecting both larval and adult stages in the ETP and CG. The extreme lateral heterogeneity of the ETP mixed layer compared with the lateral homogeneity of the CG mixed layer may in part explain larval depth distribution differences. Laterally continuous isothermal layers (i.e., 15-20°C) and density surfaces within the ETP thermocline may provide larvae with more suitable uniform physical environments not present in the mixed layer. Also, the shallow and more intense oxygen minimum layer in the ETP may exclude spawning populations of some species. Large differences in the vertical distribution of primary productivity and macrozooplankton concentrations could affect both the

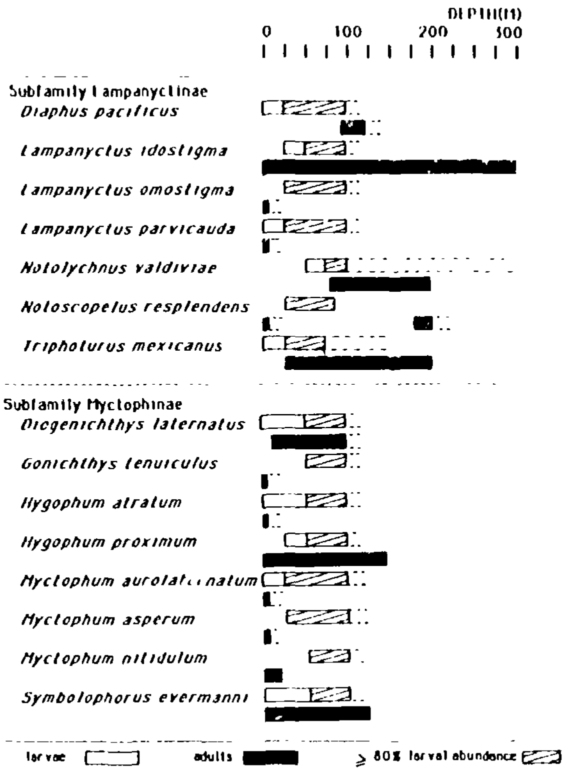

Fig. 3 Larval (upper bar) and juvenile and adult (lower bar) nighttime depth distributions for the more abundant lampanyctine and myctophine (Myctophidae) species taken in the North Pacific central gyre during late summer. Hatched larval depth range indicates depth intervals where >90% of the estimated 0-600m water column abundance occurred. Adult depth distributions from Clarke (1973).

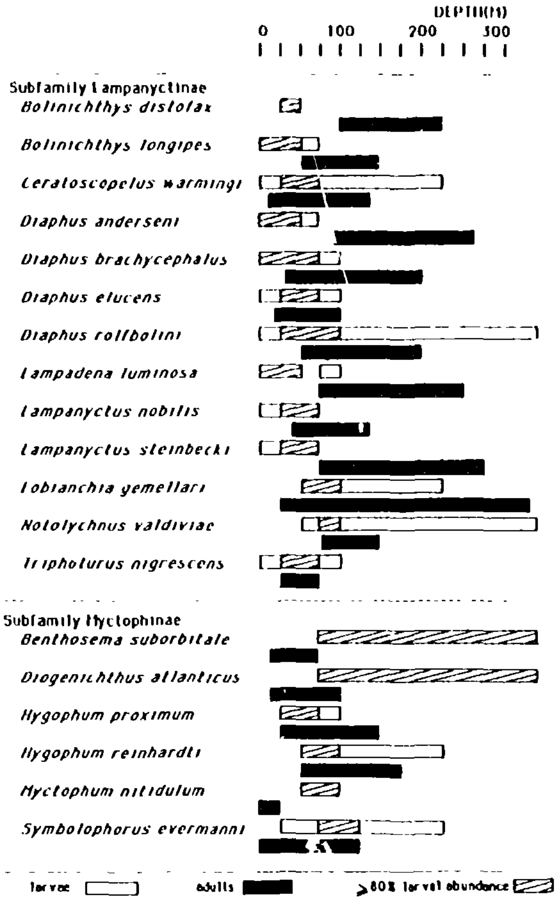

Fig. 4 Larval (upper bar) and adult (lower bar) nighttime depth distributions for the more abundant lampanyctine and myctophine (Myctophidae) species taken in the eastern tropical Pacific during late summer. Hatched larval depth range indicates depth intervals where >80% of estimated 0-100m abundance occurred. Dashed lines for both larvae and adults indicate probably deeper distributions. Adult depth distributions from Robison (1973) and Wisner (1976).

larval and adult stages. In the ETP large macrozooplankton concentrations occur both day and night within the mixed layer and often at the surface in conjuction with high primary productivity rates; macrozooplankton abundance is relatively low at depths >150m (Longhurst, 1976). These concentrations could directly affect the adult assemblage by providing a selective advantage to predatory species migrating into surface layers to feed and could affect larval distributions through increased competition for food and/or predation relative to deeper areas. Nocturnal predatory activities of the migratory adults could also provide a selective advantage for deeper living larval stages. In contrast, overall low water column productivity and more evenly distributed macrozooplankton biomass through the upper 600m of the CG (McGowan & Walker, 1979) probably offer a selective advantage to moderate or low energy migrators and non-migrating species with larvae in the lower mixed layer below depths of modestly increased night zooplankton biomass and above adult predatory activities.

DISCUSSION

These observations on larval and adult fish vertical distributions and species compositions relative to overall values and vertical distribution of primary productivity are supported by the results of multidisciplinary studies made across the eastern equatorial Pacific (97°W to 155°W) by Soviet scientists during Cruise 17 of the R/V "Akademik Kurchatov". Sorokin et al. (1977) reported highest primary productivity rates in the east (97°W) with maximum chlorophyll concentrations, phytoplankton biomass and photosynthesis rates within the shallow mixed layer and upper thermocline. Progressing westward, the mixed layer deepened, nutrient levels and primary productivity values decreased, and chlorophyll and phytoplankton biomass values became more evenly distributed through the upper water column (0-100m). Associated with east to west changes in primary productivity were: 1. decreasing, deepening and more evenly distributed values of net- and macrozooplankton biomass (Timonin & Voronina, 1977; Parin, 1977); 2. decreasing vertical migration activity by net- and macro-zooplankton and mesopelagic fishes (Timonin & Voronina, 1977; Parin, 1977); 3. increasing myctophid species diversity due to increasing numbers of nonmigrating lampanyctine species (Parin, 1977); and 4. increasing proportions of total (0-250m) larval fishes occurring in the mixed layer relative to thermocline and deeper waters (Gorbunova, 1977).

CONCLUDING REMARKS

These comparative studies indicate the value of vertical distribution information for both larval and adult stages in understanding geographic differences in the composition of mesopelagic fish assemblages. They also indicate the necessity of coincidental information on the vertical distributions of other biological and physical parameters and similarity or standardization of sampling techniques to permit interregional comparisons of data sets.

At present there are few oceanic ichthyoplankton assemblage studies on which to base ecosystem comparisons. This is in part due to past species identification problems, but recent advances in larval fish taxonomy (Blaxter, 1984) have greatly reduced this problem. Similarly, there have been few multidisciplinary studies relating adult and larval fish vertical distributions to other biological and physical parameters. This is attributed to the lack of adequate and reliable depth stratified sampling devices. Development of the Manta neuston net has made possible quantitative sampling of the at times very important surface layer. Additionally, recent development of electronically controlled net systems such as MOCNESS and BIONESS (Wiebe et al., 1976; Sameoto et al., 1980) have resolved problems of taking replicated quantitative samples at known and controllable depths intervals. Attached environmental sensing systems permit simultaneous collection of important physical data. Additional attached devices (e.g., photometers, acoustics sounders, particle counters, fluormeters, and net release triggered niskin bottles) will allow quantitative description of other environmentally important factors associated with net catches. With these net systems we have the ability to adjust vertical sampling intervals to biologically important parameters (e.g., mixed layer and thermocline depth, chlorophyll maxima, isolumes etc.) based on real-time shipboard displays rather than relying on fixed and arbitrary sampling intervals which often overlap and obscure their significance. The largest problem now facing such descriptive biological oceanography/pelagic biogeography studies is obtaining necessary funding.

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GENETICS, LIFE HISTORIES, AND PELAGIC BIOGEOGRAPHY

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INTRODUCTION

Biogeography is the study of the distribution and abundance of organisms. Studies of ancient patterns revealed through analyses of the fossil record provide insight into present day patterns of higher taxa (e.g. families). Contemporary distributions at the species level can be used to provide insight into evolutionary processes and the mechanisms of speciation in the sea.

Present day patterns of distribution and abundance of species represent the outcome of interactions between intrinsic and extrinsic factors. The intrinsic component lies in the genetic structure of the species, and reflects adaptation to the current environment, as well as the genetic constitution of the species' ancestors. Extrinsic factors include physical and chemical features of the environment such as temperature and salinity, and biological features such as competitors and predators. The distribution and abundance of a species is not a static property The changes that occur reflect variation in the intrinsic and extrinsic factors.

The aim of this paper is to emphasize the importance and connections between the genetics, life histories, and biogeography of marine holoplanktonic organisms. I have chosen to limit my discussion here to the group that I am most familiar with, namely the copepods. Whenever possible I will extend my arguments to include other groups as well. Most studies which deal with the population dynamics of marine planktonic copepods involve the examination of only a small spatial or temporal subset of the species. The extent to which such data are representative of the whole species is rarely considered. Such research has primarily involved cohort analyses of field populations (Colebrook, 1982; Landry, 1978; Corkett & McLaren, 1978; and many others), and laboratory studies of the influence of environmental factors (e.g. temperature, salinity, food quantity and quality) on biological traits (e.g. growth, development, reproduction, life span, excretion, respiration and feeding) (Dagg, 1978; Vidal & Whitledge, 1982; and many others). Very few studies have addressed the relative importance of genetic factors in regulating the population dynamics of holoplanktonic taxa.

DISCUSSION

The two major approaches used to gain insight into the genetics of marine species have been electrophoresis and quantitative genetics. Electrophoretic analyses of enzymes have provided insight into the population genetics of a variety of marine organisms including echinoderms, crustaceans, polychaetes, molluscs, coelenterates, and fish. Reviews by Burton (1983), Koehn (1984), and Nelson & Hedgecock (1980) provide excellent summaries of the work on invertebrates. The majority of these studies however, deal with benthic animals that have a meroplanktonic larval stage. Relatively few studies have involved holoplanktonic organisms. A weakness of electrophoresis is that the adaptive significance of the different electromorphs (i.e. mobility variants) is seldom known, so that their importance in the evolutionary process and speciation is difficult to assess. Moreover, the relevance of different electromorphs to population growth is not clear.

A few studies have addressed these problems in recent years. For example, biochemical studies have shown that the functional properties of allozyme variants are different (Hoffman, 1981 for *Metridium senile* a sea anemone; Burton & Feldman, 1983 for *Tigriopus californicus* an harpacticoid copepod; Hilbish & Koehn, 1985 for *Mytilus edulis* a bivalve). Moreover, for

Tigriopus (Burton & Feldman, 1983) and *Mytilus* (Hilbish et al., 1982) respectively, it has been demonstrated that allozyme variants of glutamate-pyruvate transaminase and aminopeptidase-1 differentially affect cell volume and thus tolerance to osmotic stress via the regulation of intracellular amino acid concentrations. Other evidence relevant to this problem comes from the apparent relationship between heterozygosity and growth rates in oysters (Koehn & Shumway, 1982) and mussels (Koehn & Gaffney, 1984). Although it has been argued that the high growth rates are due to the increased metabolic efficiency of heterozygotes, the mechanism underlying the relationship has not yet been clarified.

Quantitative genetics is designed to show levels of heritable variation for traits related to population growth i.e. fecundity, development time, mortality, age at maturity, life span, body size (Falconer, 1981). This is an approach that has been used for decades by breeders of domesticated plants and animals. It provides an estimate of the heritability of a trait, which is the ratio of the additive genetic variance to the total phenotypic variance for the trait. Knowledge of the heritability of a trait can be useful in predicting the response of the trait to selection, and thus the potential for evolutionary change. The rate of change may, however, be subject to constraints relating to pleiotropy, linkage, and environmental interactions (Falconer, 1981). Since this approach requires the breeding of individuals under controlled conditions, relatively few marine species have been analyzed. Most studies have involved small crustaceans with relatively short life spans, and mollusc species that are important in aquaculture. Studies by McLaren, Corkett, and Bradley and colleagues on marine planktonic copepods indicate the existence of large amounts of heritable variation for traits that are closely related to population dynamics (e.g. body size, physiological tolerance, age at maturity) (see review Bradley 1982; McLaren, 1976; Marcus, 1985). The maintenance of high levels of genetic variation suggests that selection may assume an important role in determining the expression of these traits under natural conditions. The maintenance of high levels of variation could be due to temporally or spatially varying selection pressures, coupled with short generation times, since the abundance of many marine zooplankters fluctuates seasonally, and many species have very extensive geographic distributions.

To date genetic studies have led to the formulation of several general concepts concerning the maintenance of genetic variability, and how species cope with environmental heterogeneity on temporal and spatial scales (see references in Battaglia & Beardmore, 1978; Nelson & Hedgecock, 1980). In regard to the pelagic marine environment theory predicts that the genetic variability of neritic species should generally be low whereas the genetic variability of oceanic species should be high. The predicted difference is attributed primarily to the greater instability of coastal waters due to waves, currents, tides and seasonal changes. By maintaining only a few broadly functioning alleles it has been proposed that species are better able to cope with such environmental variability. Within regions the different life history patterns of species probably contributes to different levels of genetic variability. For example in temperate coastal waters which undergo marked seasonal variation some species may respond to the temporally changing environmental conditions with long lived individuals that are able to tolerate the changes with a few broadly functioning alleles. Other species with short generation times and high genetic variability might respond with different individuals (i.e. genetic combinations) favoured in each generation. Thus, short lived copepods such as *Acartia* spp. which undergo several generations during one year should be more variable than longer lived species such as *Calanus spp.*

It has long been recognized that many marine planktonic organisms have very broad spatial distributions which often encompass an extensive horizontal and vertical gradient (see Van der Spoel & Pierrot-Bults, 1979). Broad horizontal distributions have largely been attributed to their potential for dispersal across great distances in ocean currents. Despite evidence of phenotypic differences in morphological, physiological, and/or behavioral traits between populations from distant areas, it was initially believed that holoplanktonic species were genetically homogeneous due to the potential for considerable panmixis. Consequently, the observed phenotypic differences were often ascribed to environmental modification, and phenotypic plasticity The results of several studies on benthic invertebrates with long lived planktonic larval stages (recent review by Burton, 1983) and a few studies of pelagic copepods and euphausids (see references cited above; Marcus, 1984, 1985; Bucklin & Marcus, 1984; Fevolden, 1984) indicate that this assumption is not valid; temporal and spatial genetic variability have been documented in these groups. Further work is necessary to quantify and establish the significance of this variation.

CONCLUSIONS

Revealing the genetic basis of this phenotypic variation is necessary to understand the mechanism(s) which enable species to adjust to environmental change, the potential importance of emigration in the re-population of foreign areas, and the evolutionary steps that are basic to speciation. Genetic studies are of fundamental importance to biogeography. There are many problems that need to be addressed. These include:

1. the relationship of life history, population structure, and genetics to speciation;
2. the relationship of dispersal and genetic structure of species;
3. the relative importance of population size (drift) and selection in effecting evolutionary change;
4. the functional properties of different allele products;
5. the relationship between genetics and bioenergetics to determine whether genotypes are differentially adapted to food regimens.

Although genetics probably plays only a small role in directly determining changes at higher levels of organization (e.g. communities and ecosystems), it assumes an important role at the level of populations (Anderson, 1983). Short term changes are recognized as adaptation; long-term changes appear as evolution and are eventually reflected at the higher levels of organization.

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WHAT CONSTITUTES AN OPEN-OCEAN POPULATION?

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INTRODUCTION

Angel(1977), in assessing limitations to the measurement of ecological parameters in the mesopelagic environment, concludes: Thus in ecological studies for which long time series are required, there may be insuperable temporal limits to processes that can be observed in situ. There have, however, been a number of successful demographic studies made using samples taken in time series. The growth rates of *Sergestes similis* and *Euphausia pacifica* have been determined off Oregon and Southern California (Pearcy & Forss, 1969; Smiles & Pearcy, 1971; Brinton, 1976; Omori & Gluck, 1979). Genthe (1969) also obtained a valid time series of samples of *S.similis* but from the more prescribed Santa Barbara Basin, as did Omori et al. (1973) of *S. lucens* within Suruga Bay, Japan. Comparable studies of fish included those on the myctophid *Benthosema glaciale* by Halliday (1970) to the south of Nova Scotia and by Kawaguchi & Mauchline (1982) in the Rockall Trough in the North East Atlantic.

Thus time series of samples extending over a year or longer and resulting in meaningful demographic analyses can be obtained in some oceanic regions, at least in the proximity of continental slopes. This paper examines sample time series from one such slope region, the Rockall Trough in the northeastern Atlantic, and discusses some potential implications in biogeography.

THE TIME SERIES OF SAMPLES

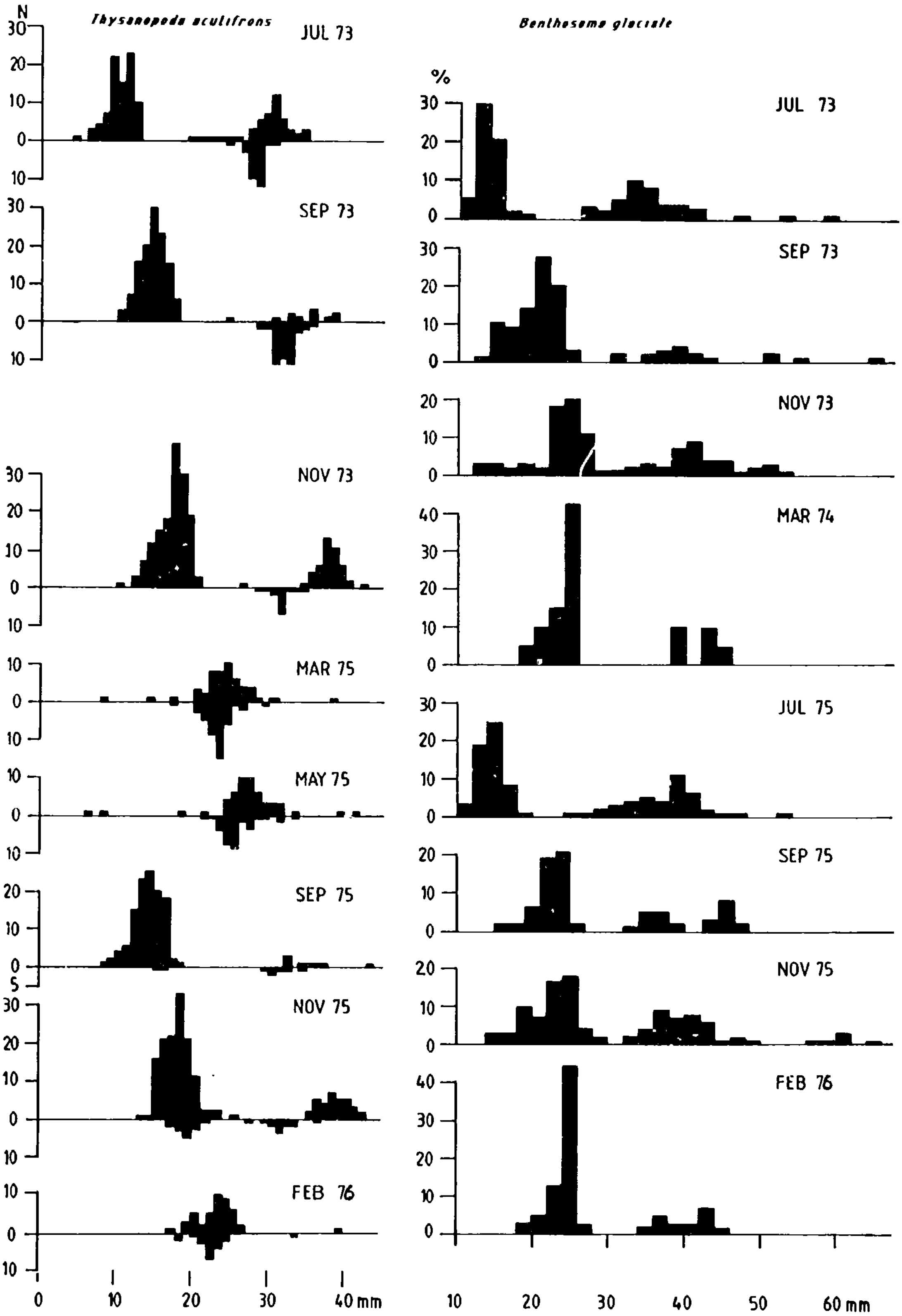
Samples were collected by Combination Rectangular Midwater Trawls 1+7m^2 mouth areas (Baker et al., 1973; Roe et al., 1980). The nets were fished open to depths between 2000 and 2600m where they were towed horizontally for four hours. This horizontal fishing transect is deeper than the bathymetric distributions of the euphausiids and mesopelagic fish discussed here. The hauls, therefore, provide oblique samples of these organisms. Samples were collected at two monthly intervals between July, 1973 and March, 1974 and between March, 1975 and February, 1976 close to 55°N 12°W (Mauchline & Kawaguchi, 1982) Supplementary samples were collected throughout the rest of the Trough and on the Scottish continental shelf and the Rockall Bank.

RESULTS

Body length—frequency histograms for the euphausiid *Thysanopoda acutifrons* and the myctophid *Benthosema glaciale* are shown in figure 1. Two time series of samples are represented in each species. Coherent histograms extend for four months, July to November, 1973 in both species. There is evidence of coherence in *T.acutifrons* from March 1975 to February, 1976, a period of 11 months. In *Benthosema glaciale* the histograms of July to November, 1975 are coherent but that of February 1976 is different.

Similar histograms have been obtained for *Lampanyctus macdonaldi* and *Protomyctophum arcticum* by Kawaguchi & Mauchline (1982) and for *Maurolicus muelleri* and also for the euphausiids *Meganyctiphanes norvegica, Thysanoessa longicaudata, Nematoscelis megalops, Nematobrachion boopis* and *Stylocheiron*

Fig. 1 Length/frequency histograms from time series of samples from the Rockall Trough of the euphausiid *Thysanopoda acutifrons* and the myctophid *Benthosema glaciale*. Those of *B.glaciale* after Kawaguchi & Mauchline (1982). Juvenile and female euphausiids above the line, males below the line.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JUL 75
SEP 75
NOV 75
FEB 76
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60 mm

maximum. Histograms of *Euphausia krohni* and *Stylocheiron longicorne*, although frequently presenting clearly defined modes, are irregular and defy interpretation.

Plotting of the numbers of individuals of *Thysanopoda acutifrons* and *Benthosema glaciale* occurring in the oblique hauls produces curves that correspond with regular seasonal changes in population numbers expected from the seasonal periods of breeding (Fig. 2).

DISCUSSION

Modes can be followed through the time series of samples of euphausiids and fish. The regularity of seasonal changes in numbers of individuals correspond with seasonal periods of reproduction and lack of reproduction. Such features in time series samples infer that the same populations of the species are being repetitively sampled. This repetitive sampling seems to be effective in the Trough over periods of six or more months.

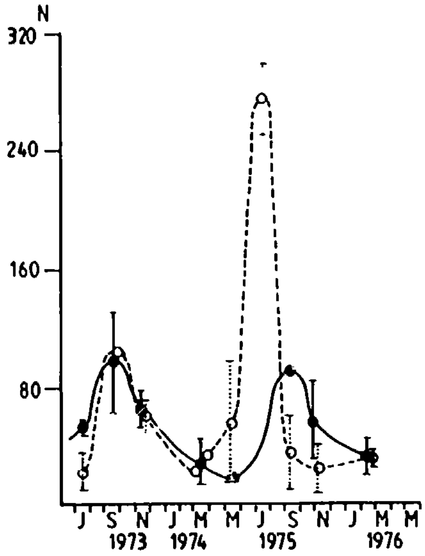

Fig. 2 Seasonal changes in the mean numbers of *Thysanopoda acutifrons* (dots and solid line) and *Benthosema glaciale* (triangles and hatched line) in samples from the Rockall Trough. Standard deviations are shown where three or more samples are available.

Are there hydrographic features within the Rockall Trough that can confer a residence time on a group of organisms of a species such that they can form a population? There is a general northeastward drift through the centre of the Trough (Fig. 3) at a velocity of 2 to 5cm sec^{-1} (Booth & Ellett, 1983). A passively carried organism would therefore require 2.5 to 6 months to travel from the proximity of 54°N to the Anton Dohrn Seamount. There are opposing slope currents extending to depths of 700m on either side of the drift (Booth & Ellett, 1983). The currents are some 10km in width and have velocities of 16 $\pm$ 5cm sec^{-1}. Mixing takes place

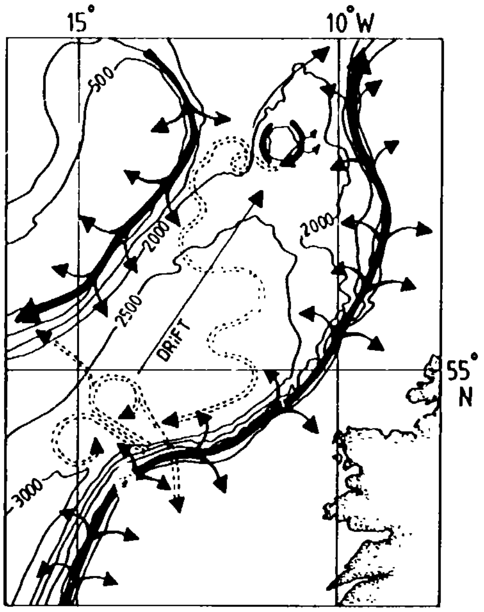

Fig. 3 Present concepts of the hydrography of the upper 700m of the Rockall Trough. The directions of the slope currents on the east and west sides and that of the general north-eastward drift are shown. Arrows on the slope currents indicate mixing and those on the deep-water side of the currents [illegible] possible shedding of eddies. The anticyclonic circulation around Anton Dohrn Seamount is over its slope and eddies are shed eastwards. Hatched lines show less permanent features such as possible current paths as detected by sub-surface drogues. (Booth, Ellett & Meldrum, unpubl.)

along the edges of these currents and eddies can be shed from them into the Trough.

A sub-surface droque (at 116m depth) meandered southwards through the Trough, presumably in a series of eddies, against the general northeastward drift (Fig. 3) (Booth & Meldum, 1984). There are thus mechanisms for the formation and retention of populations within this region, certainly for periods of three to six months, the duration of coherence commonly found within the histograms (Fig. 1).

Populations of myctophids and euphausiids aggregate, some species very strongly at certain seasons. Aggregated individuals, as opposed to dispersed, are more likely all to experience the same hydrographic circumstances in a mixed region such as the Rockall Trough. Their expatriation could occur irregularly but would result in movement of populations (large numbers of individuals) rather than single individuals. Expatriate areas of oceanic species from the Trough are defined (Fig. 4) from the data of Einarsson (1945) Oestvedt (1955), Dahl (1961), Fraser (1968) and Wiborg (1968). Wiborg describes populations of oceanic species of euphausiids in Norwegian fjords that have been introduced by influxes of Atlantic water. He considers that 'the populations are supplied from outside at more or less regular intervals'. The mechanism by which this will take place is shown in figure 4.

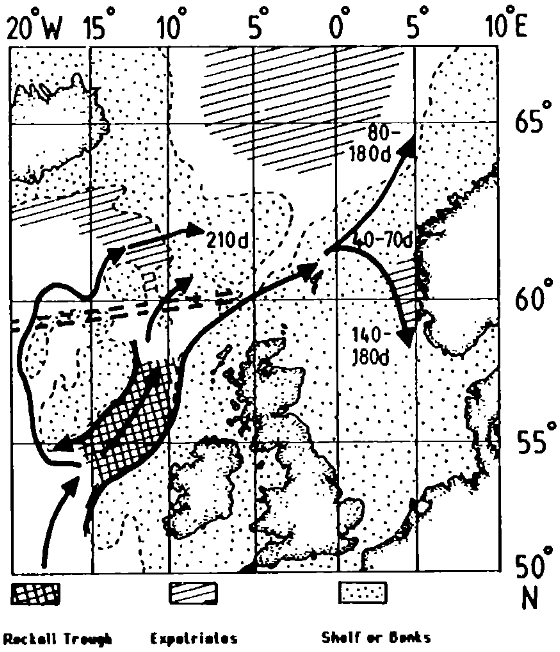

Fig. 4 Recognized expatriate areas of oceanic species from the Rockall Trough. Routes and travel times (days) determined by sub-surface drogues are indicated. The easternmost segment of the boundary between the subarctic and temperate faunal provinces (Backus et al. 1977) is shown hatched between 59°N, 20°W and 60°N, 5°W.

Backus et al. (1977) draw the easternmost segment of the subarctic-temperate boundary arbitrarily by using the 9°C isotherm at 200m depth between 59°N, 22°W and 60°N, 5°W (Fig. 4). The northern breeding limits of a number of species, however, appear to be south of this, between about 50°N and 58°N. Further, the relatively large scale expatriation of oceanic species north and north-eastwards from the Trough to latitudes as high as 65°N and on a more or less regular basis suggests some modification of the concept of the easternmost segment of this boundary. The northeastward slope current can act as a "pump" to inject temperate oceanic species towards the Norwegian Sea and allow maintenance of populations outside the principal biogeographic range of the species. Oceanic species can also be advected in the southward slope current round the Rockall Bank and reach the Iceland and Norwegian Basins. This situation at the easternmost segment of the subarctic-temperate boundary of Backus et al. (1977) reinforces the concept of plasticity in some areas of such projected boundaries.

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THE BIOGEOGRAPHY OF PELAGIC ECOSYSTEMS

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INTRODUCTION

During the decades 1950 to 1970 a large number of wide ranging oceanographic expeditions explored the Pacific Ocean. These often included the systematic sampling of macrozooplankton in the upper 200m or so. The resulting collections of many thousands of samples provided the basis for the mapping of species patterns in the epipelagic zone. Many deeper net tows were also included in these collections but their sampling intensity was much less, so that the determination of pattern for deeper living organisms is considerably less certain. Although the expeditions and cruises were often done in different seasons and years in different areas, it was possible to make composite maps of species abundance which included both positive and negative records. Both records are essential in the mapping of any entity that does not have a continuous distribution (for example: species vs. biomass) and whose abundance may be influenced by environmental processes and events. It is important in the interpretation of species pattern to know if blank areas are blank because of lack of sampling or because an appropriate attempt to find the organism failed. Thus it is critical to have a large number of samples available for analysis. The expedition collections were also, for the most part, quantitative. This means that relative abundances can be estimated and gradients and smaller scale variations within the larger range patterns determined. Because of this detail it is possible to interpret the resultant maps of abundance, rarity and absence, in ecological terms and thus help us understand the conditions under which oceanic populations vary.

A number of researchers have, fortunately, taken this quantitative approach and we now have a basic framework of biogeographic pattern for the Pacific, that is amenable to ecological and oceanographic interpretation (Bieri, 1959; Bradshaw, 1959; Bowman, 1960; Alvariño, 1962; Brinton, 1962; Nemoto, 1962; Fager & McGowan, 1963; Brodsky, 1965; Frost & Fleminger, 1968; Beklemishev, 1969; Venrick, 1971; Okada & Honjo, 1973; Reis et al., 1978; McGowan & Walker, 1985). I have summarized these patterns in two earlier papers and so have Reid et al. (1978). Among other attributes, two of their features stand out;

1) There is a large amount of agreement across higher taxa as to the shape of the patterns. That is, there are copepod species patterns that look like those of euphausiids, pteropods or thaliaceans. A careful statistical analysis agreed with simple visual observations of the maps, that there is significant spatial co-occurrence of species (Fager & McGowan, 1963).

2) The patterns of most species assemblages strongly resemble those of the major circulation-recirculation systems of the Pacific. The gradients and major frontal zones delineating these circulation systems were determined independently of those of the ranges of species assemblages and yet there is excellent correspondence.

Why should evolutionary adaptation have resulted in such a picture? We cannot investigate this problem experimentally but there are observations that may increase our understanding.

The North Pacific Subarctic cyclonic gyre and water mass; The Central North Pacific anti-cyclonic gyre and water mass; The Eastern Tropical Pacific, part of the great Equatorial circulation-recirculation system of the tropical Pacific (Fig. 1) have been studied, as systems, long enough so that their structure and function may be compared. We can now ask how these three provinces differ and in what ways are they similar? In other words what is the empirical evidence for the oceanic habitat characteristics that are (were) important in evolution?

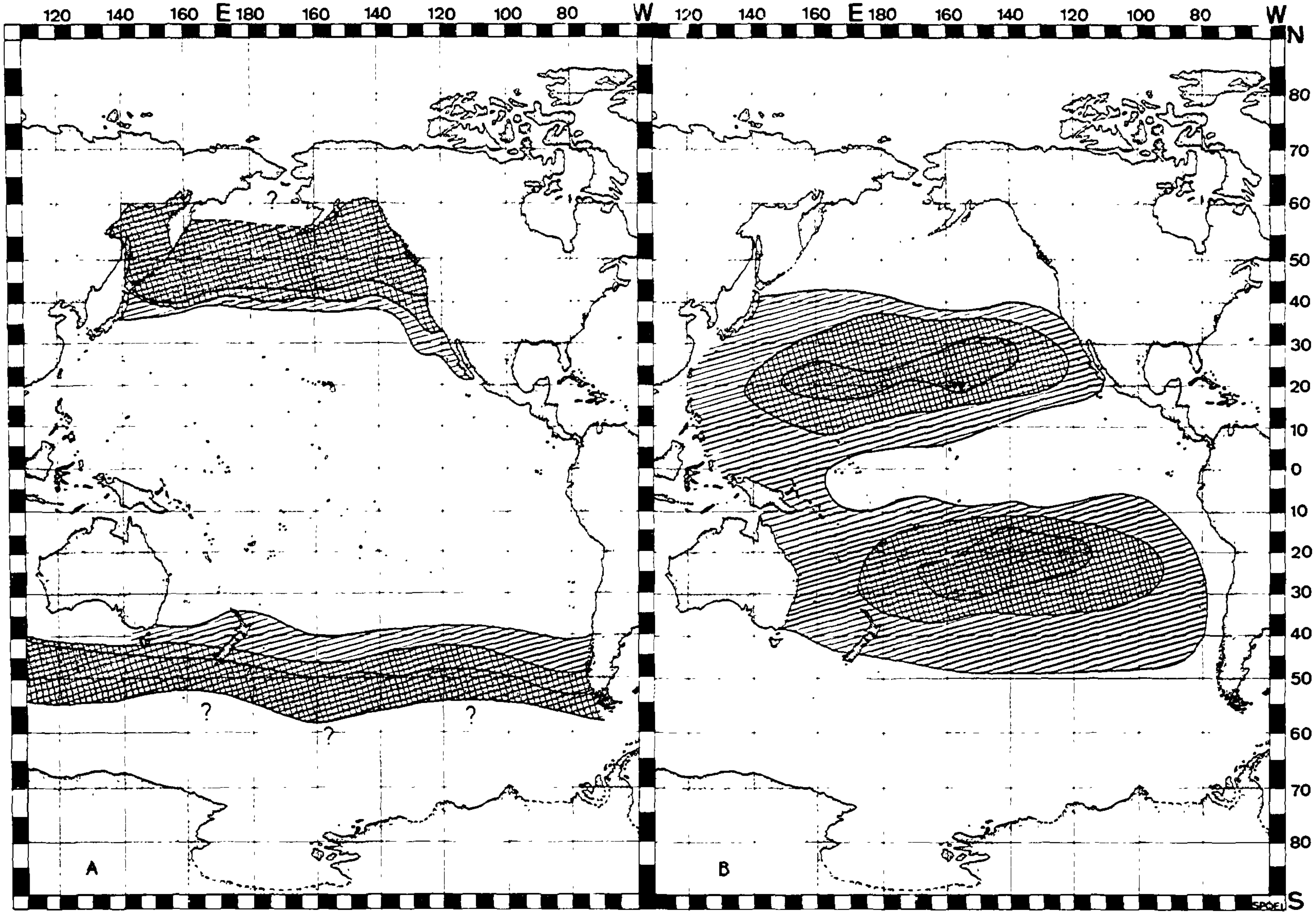
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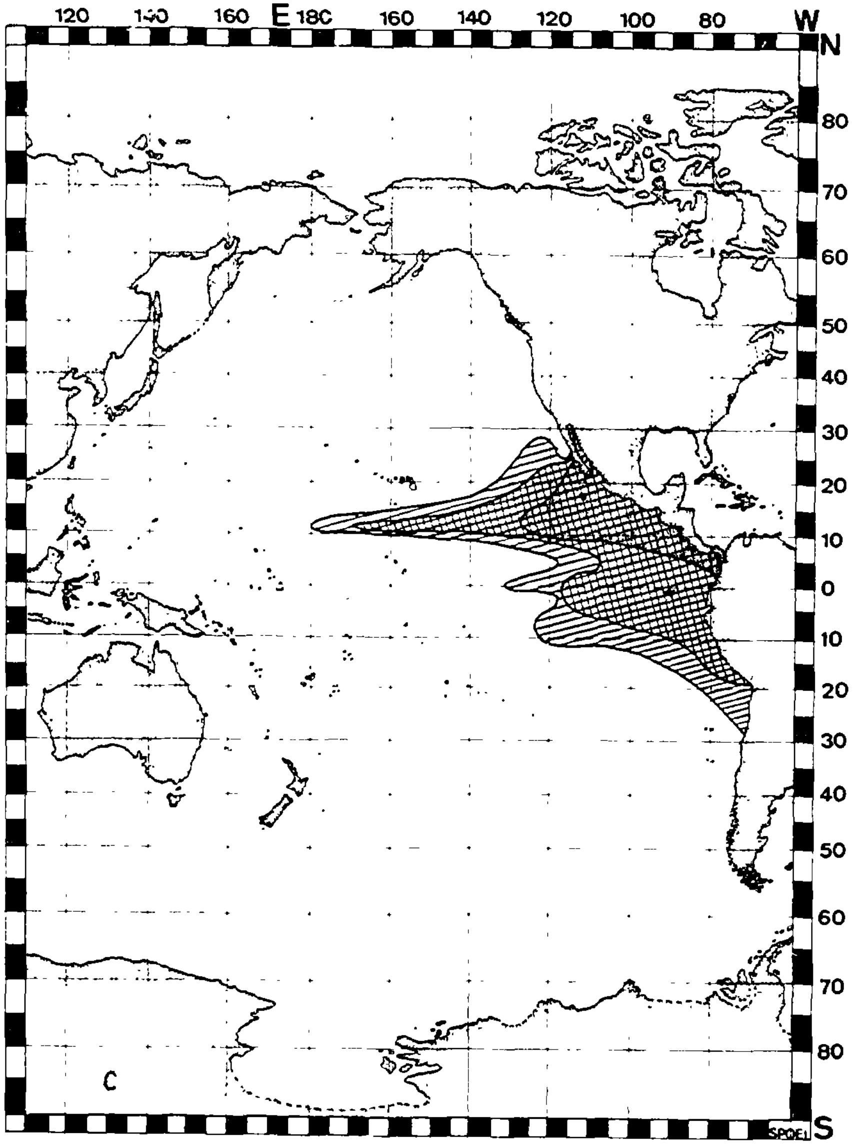
Fig. 1 A: The Subarctic and Subantarctic Pacific faunal provinces. B: North and South Pacific Central Gyre faunal provinces. C: Eastern Tropical Pacific faunal provinces. (after McGowan, 1974) Lighter shading indicates boundary zones.



THE NORTH PACIFIC SUBARCTIC GYRE

This is a cyclonic circulation system (Fig. 2) with the salient feature of all such systems; massive upward movement of deep water in its centre. Evidence for this process may be clearly seen in vertical sections of the eastern Subarctic where the isopleths of density, temperature, salinity and plant nutrients all bend upward (Dodimead et al., 1963; McGowan & Williams, 1973)(Fig. 3).

The salinity structure of this region differs strongly from the waters to the south. The Subarctic is a climatic region where precipitation and runoff exceeds evaporation and thus its upper layers are relatively fresh. But there is a strong halocline separating this upper layer from the lower zones (Fig. 3). Because of the excess of precipitation one might expect the upper layers would become progressively fresher. This does not occur because of the input of deep salty water from upwelling in the centre of the system and because a large fraction of the surface waters of the southern limb of the circulation, the North Pacific Drift, turns to the south as it nears the North American continent and contribute its cool, fresh, nutrient-rich water to the California Current. This water and its constituents are not recirculated back into the Subarctic system. The southern edge of this system is evident in figure 3 where, at about 43°N the halocline disappears. The disappearance of this characteristic feature is due to the rapid, spatial change in the climatic and hydrographic mechanisms that are responsible for its maintenance.

There are very strong seasonal cycles in both hydrography and biology and this sets the region apart from others in the Pacific. This climatic seasonality results in a large annual excursion in mixed layer temperatures (about 5°C to 14°C at 50°N, 145°W). Mixed layer depths vary from about 20m in August to about 100m (the top of the halocline) in January. At these latitudes there is also a large excursion in the depth of light penetration, out of phase with that of the mixed layer. The result is a brief period in the spring when the critical depth exceeds the mean mixed layer depth (Parsons et al., 1966); this leads to a burst of productivity and zooplankton growth and a large, seasonal change in zooplankton biomass (Miller et al., 1984). Such large scale and consistent structural and functional features in a

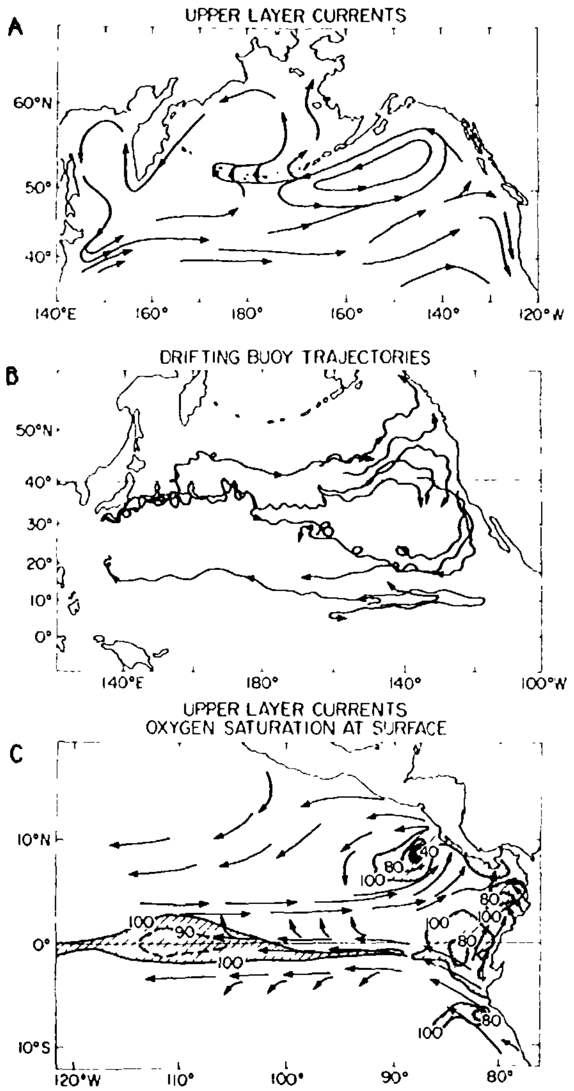


Fig. 2 A: The gross circulation of the upper zone of the Subarctic Pacific (after Dodomead et al., 1963). B: The trajectories of satellite tracked drifters showing the large anti-cyclonic gyre in the eastern half of the central North Pacific (after McNally et al., 1983). C: The gross circulation of the upper zone of the Eastern Tropical Pacific and percent oxygen saturation at the surface showing upwelling centres (after Eastropic Atlases vol. 2, 1971 and vol. 6, 1972).

dynamic system are obviously driven by powerful forces of climate interacting with the characteristics of the locale, such as basin shape, topography and latitude.

Within the larger Subarctic system there are several cyclonic sub-systems (Fig. 2). Although they have not been studied as has the Gulf of A[illegible]a sub-system, we can assume, because of the [illegible]e of the circulation and the doming up of property concentrations (Dodimead et al., 1963). that they also function as upwelling centres. Thus the Subarctic system is not a simple functional or uniform unit but consists of several similar sub-units imbedded in the larger regional system. This, within system, variability in structure may affect biological processes and aspects of pattern, for in an earlier study it was shown that there were several loci within the Subarctic where there was a substantial abundance concordance among the individual species populations (Fager & McGowan, 1963). But these localized areas do not harbour unique species assemblages or endemics, and it is my guess that they are so variable in their intensity and perhaps locale that they are too "unpredictable" to have served as habitats or centres for diversification where selection for specialized genepools could proceed uninterrupted for the requisite number of generations.

The Subarctic species differ greatly from others in their behaviour and life history patterns as well as morphology. The copepods have been most intensively studied and their populations have been shown to have seasonal cycles of migratory behaviour, reproduction and growth which are very closely keyed to the large scale seasonal hydrographic processes that are so evident in this area (Miller et al., 1984). Further a substantial fraction of the populations of all of the Subarctic plankton must "emigrate" from the system along with the southward flowing Subarctic water that becomes part of the California Current. This loss must be a important source of mortality and a regular feature of the population dynamics of the species; one to which they must have adapted.

The Pacific Subarctic pelagic zone is a rich ecosystem in terms of annual production and sustained high standing stocks but it is poor in species of plankton (and probably fish and squid) (Reid et al., 1978). That is; it is a high productivity, high biomass, strongly seasonal, low diversity system.

THE CENTRAL GYRE OF THE NORTH PACIFIC

The contrast between the North Pacific Central Gyre and Subarctic could hardly be greater

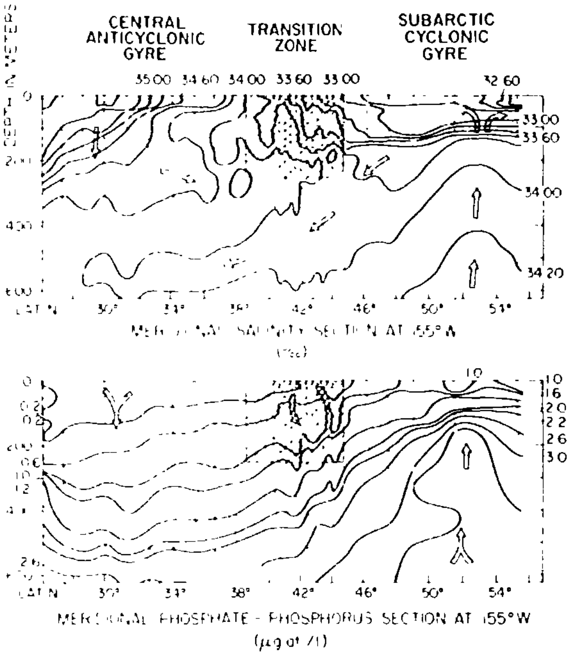


Fig. 3 Upper: A north-south transect of the North Pacific at 155°W (Kodiak to Hawaii) showing salinity values. North of about 44°N a well developed halocline can be seen at 100m. South of about 38°N a shallow halocline is present at about 40m. Between these two lies the "Transition Zone" an area of fronts, inversion and instabilities. Arrows indicate the inferred direction of vertical movement, upwelling and sinking.
Lower: The same north-south transect as above showing the phosphate concentration. Areas of upwelling in the Subarctic Gyre and vertical mixing in the Transition Zone are indicated by arrows. The upturned isopleths and high surface values are consistent with the upper panel. South of the Transition Zone, low surface nutrients and downturned isopleths are consistent with the expectation of generalized downwelling (after McGowan & Williams, 1973).

although the two systems are contiguous. The gross circulation in the Central Gyre is anti-cyclonic and hence there is a generalized sinking of waters in the interior regions (Fig. 2). The mixed layer temperatures are much higher than those of the Subarctic ranging from about 18°C in winter to 24°C in summer. The mixed layer depths in the Central Gyre vary from a February mean of about 120m, but with broad limits to a mid-summer mean depth of about 40m with narrow limits. There is a halocline in this gyre but the more saline water is in the upper layers with fresher waters underneath (Fig. 3) and there is a seasonal change in its depth. This is a climatic area where evaporation exceeds precipitation and there is virtually no runoff. The nutricline is deep at well over 100m and does not appear to change seasonally. Most of the chlorophyll in the watercolumn is concentrated in a deep (about 110m) chlorophyll maximum whose depth seems seasonally invariant. The primary productivity maximum is broad but peaks at about 50m both in winter and summer. No seasonal changes in productivity have been detected. Both phyto- and zooplankton biomass are very low and, as might be expected, there is no detectable seasonality in zooplankton abundance (Hayward et al., 1983; Hayward & McGowan, 1985).

Biologically, the Central Gyre is highly divers. It is the most species-rich province in the Pacific (Reid et al., 1978), its dominance hierarchy is very persistent and its community structure quite stable (McGowan & Walker, 1985). The intensity of patchiness, on all scales, is low (Hayward et al., 1983). There is no evidence for the type of within system sub-units that occur in the Subarctic.

Thus the Central Gyre is a low productivity, low biomass, non-seasonal, high diversity, relatively homogeneous system.

THE EASTERN TROPICAL PACIFIC

Although this region can be considered to have its own, unique circulation scheme it was not characterized as a separate entity by Sverdrup et al. (1942), but rather included as merely a part of the gigantic Pacific Equatorial water mass. This may have been due to a lack of appropriate data, at the time they wrote, or perhaps it was felt that the continuity between the circulation of this region and the rest of the Equatorial zone was too great to warrant it being set off as a separate system with natural boundaries and distinctive in situ processes and events. However, we now know this region does have and indigenous fauna and further, some species found throughout the Equatorial water mass are absent or rare here. Thus populations do "recognize" it as a special habitat in the same sense that they "recognize" the Pacific Subarctic and Central circulation systems.

The region has some highly distinctive physical processes and hence environmental structure, that set it apart. For example; the Costa Rica dome is a massive cyclonic gyre near 9°N 88°W caused by the reflection of the Equatorial Counter Current to the west (Fig. 2). Sea surface oxygen saturation values are low in the centre of this region presumably because the water has so recently welled up that it has not yet equilibrated with the atmosphere. Hydrographic transects show the spectacular doming upward of isopleths of all properties (Fig. 4)(Eastropac Atlases 1970-1975). Chlorophyll and primary productivity measurements show the area to be one of the most productive anywhere in the worlds tropics (Owen & Zeitschel, 1970). In addition to this remarkable dome feature there are episodic but apparently large-scale, coastal upwellings in the Gulfs of Panama and Tehuantepec. Thus, just as in the Subarctic, there are important sub-units within the system.

Variations in coastal winds are responsible for the episodic nature of coastal upwelling. The intensity of oceanic upwelling within the Costa Rica dome is also quite variable, no doubt due to seasonal and interannual changes in the strength and position of the trade wind-driven equatorial circulation system. These large-scale global winds do not neccessarily co-vary in intensity with local coastal winds. A third significant process, and perhaps a more consistent one, is the input of water from the south-east; the Peru Current's cold, nutrient rich extension along the equator (Fig. 2). These three sources of nutrient input may vary indepently in respons to forces

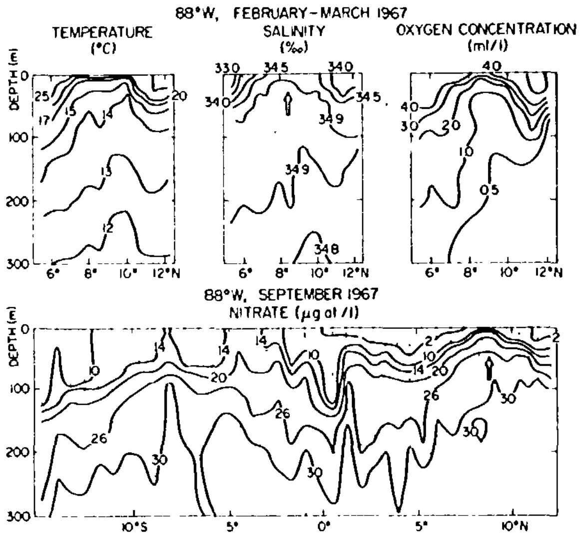


Fig. 4 Upper: The distribution of the three properties temperature, salinity and dissolved oxygen in a section at 88°W through the Costa Rica dome 8°30'N. The distribution of all three properties is consistant with the expectation of vigorous upwelling in this area.
Lower: A north-south section from 10°S across the equator and through the Costa Rica dome along 88°W. The complex distribution of nutrients in the entire euphotic zone is evident. The upturned isopleths between 6° and 10°N are further evidence for a massive upwelling centre.

which have different characteristic temporal scales of variation and which are themselves driven by different processes. This makes it a very heterogeneous but very rich system. One of the consequences of the temporal variability in the rate of nutrient input is short intense but episodic phytoplankton blooms which "escape" from the control of grazers. These blooms soon deplete the nutrients and the populations crash, leaving unexploited organic matter. Thus, large amounts of particulate detritus sink out of the euphotic zone and still at relatively warm temperatures, are rapidly decomposed by micro-organisms. This results in dissolved oxygen levels sometimes close to zero at depths of 70m or less in the area of the dome. Because of this process, the entire oxygen minimum layer is far shoaler in this province and with generally much lower oxygen concentrations than elsewhere in the Pacific (Fig. 4). This peculiar regime must have had profound effects on its resident populations and has served as a strong selective force.

The mixed layer depths in the Eastern Tropical Pacific have a complex topography with a series of ridges, troughs and domes. The layer ranges in average depths from about 25m near-shore in the Gulfs of Panama and Tehuantepec to somewhat less than 80m offshore in the more oceanic regions (Bathen, 1972). The seasonal amplitude is not great ranging from about 10 to 30m. The temperatures of the mixed layer range from 26 to 29°C with little seasonality but with strong spatial gradients. Production, however, varies by a factor of almost three between seasons. There is a broad winter-spring productivity maximum followed by a somewhat briefer, smaller summer peak. This cycle is more pronounced near-shore than offshore (Owen & Zeitschel, 1970). Annual production and zooplankton biomass may be as high as in the Subarctic Gyre (Reid et al., 1978). This region seems to be only moderately rich in species but its diversity has not been well studied and this community attribute may turn out to be as complex as is the rest of the system. The entire ecosystem may also show large interannual variations since for surface layers there were strong indications for this during the 1982-83 El Niño (Barber & Chavez, 1983).

DISCUSSION

In the Pacific, a majority of the epipelagic, oceanic species of euphausiids, pteropods, heteropods and chaetognaths strongly agree on range boundaries. That is, their biogeographic patterns are very similar. There is strong evidence that many additinal taxa of zooplankton, phytoplankton, cephalopod, fish and marine mammals have many species with similar patterns. While these large scale distributions tend to coincide, their smaller scale abundance variations may or may not. The biogeographic patterns cover regions of the ocean having unique hydrographic domains that are characterized by a continuity of water movement; that is they circulate and recirculate; and by very different climatic regimes. These circulation systems are large and few in number and all trophic levels are present within them. They appear to be self-sustaining ecosystems.

Why is it that evolutionary adaptation and speciation resulted in entire species assemblages or complete communities whose spatial dimensions and shapes resemble the large scale circulation and not the smaller scale environmental features?

Three of these circulation- or ecosystems are described here, and it should be evident from even these brief, superficial accounts of their physical-chemical functional anatomy that there are vast differences between them but considerable continuity within them. The first order differences are due to the circumstances of latitude, geography, shape of the ocean basin and global atmospheric climatic patterns. The tempo and mode of internal processes and events in these regions, such as intensity of nutrient cycling and recycling, are often brought about in different ways by different forces or they may respond differently to the same forces. For example; a general global increase in wind speed might be expected to increase the velocity and mass transport of the gross surface circulation everywhere. Under our present understanding this would be expected to increase upwelling in the central regions of the cyclonic Subarctic Gyre. But this increase in rate of input of nutrient rich water might have little effect on productivity since productivity is thought to be primarily light limited in this region. However, this same increase in circulation would cause stronger downwelling in the anti-cyclonic Central Gyre and a decrease in the upward flux of nutrients, thus decreasing productivity in this already oligotrophic, nutrient limited regime (Eppley et al., 1973). Increases in the rate of upwelling in the Costa Rica dome, Gulfs of Panama and Tehuantepec and thus a greatly enhanced primary productivity would result from the same general increase in winds. Thus the same forcing function, a simple increase in global wind speeds, would increase production in the Eastern Tropical Pacific, decrease it in the Central Gyre and have little or perhaps no effect in the Pacific Subarctic. One could create many other plausible, but untested scenarios (i.e. models) but the point is; these regions are not only structurally different but also functionally different and the nature and timing of their respons to ordinary climatic seasonality or large episodic perturbations differ as well.

We do not of course, know exactly what it is about the oceanic physical environment that results in the appearance or selection of subpopulations of organisms with different degrees of fitness or how these can become spatially isolated from one another and the isolation maintained so that further diversification can happen. But whatever the processes are, they have apparently occurred on very large scales to have resulted in the patterns we see today. That this should be so may be due to the nature of the habitat. The ocean is stirred and mixes, thus smaller scale physical features do not persist, as unique features, for very long (Stommel, 1963; Haury et al., 1978). Only the large scale structures have the degree of differentness and temporal persistance to allow the evolution to operate in a mobile, moving medium.

It seems certain that the spatial and temporal patterns of most important ecosystem properties are strongly and persistently different in the three large regions discussed. In order for these large structural differences to be maintained there must be strong functional differences as well. Some of these functional differences have already been documented. Such ecosystems, along with their own assemblage of well adapted species, should not be expected to respond to climatic forcing in the same way; indeed we already have some evidence that they do not. It follows, then, that models of pelagic ecosystem function such as those analysing the efficiency of energy transfer as a means of predicting "yield" at the higher trophic levels, or those where the attempt is to determine the processes most important in "stabilizing" the system or parts of it, must take into account the profound regional differences in structure, function and respons to climate.

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BIOGEOGRAPHY AND THE OCEANIC RIM : A POORLY KNOWN ZONE OF ICHTHYOFAUNAL INTERACTION

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INTRODUCTION

The continental slope both truncates the distribution of the oceanic meso- and bathypelagic ichthyofauna and provides the headquarters for a diverse assemblage of demersal fishes. Parin & Golovan (1976) discussed the peculiarity of this boundary zone between the pelagic and demersal ichthyofauna. The broad congruence apparent between the depths of peak abundance of oceanic pelagic organisms and slope dwelling fishes was emphasised by Marshall & Merrett (1977), with its likely trophic significance. The slope contains a wider range of physical niches than occurs in the open ocean, provided by the topographical variety of the sea-bed, together with the increased mixing effect of currents impinging upon it. Nutrient renewal resulting from such mixing has been shown to enhance phytoplankton growth along the shelf break (Pingree & Mardell, 1981), which in turn will affect the relative productivity of the upper slope. At greater depths, the increase in biomass of benthopelagic plankton distributed within the 100m stratum closest to the sea-bed, observed by Wishner (1980), probably results from similar physical processes acting on sedimentary material.

ICHTHYOFAUNAL PATTERNS ASSOCIATED WITH THE SLOPE

In broad terms much is known about the overall horizontal and vertical distributions of deep-sea pelagic fishes and their demersal relatives. Many slope-dwellers among the latter have relatively narrow bathymetric limits. They comprise an assemblage which is often geographically more restricted and different from those of the continental rise and abyss. Such long-slope 'ribbon' distribution has a pelagic counterpart in the pseudoceanic group of species (sensu Hulley, 1981), which may be sub-divided into:

-1. Obligatory pseudoceanic species, whose long-slope distribution clearly parallels that of many demersal forms, are both mesopelagic and bathypelagic fishes with affinities to either the epibenthic or pelagic communities (sensu Hulley, 1981) (Table I). The majority of mesopelagic obligatory pseudoceanic species are representatives of predominantly pelagic families (e.g. Sternoptychidae, Photichthyidae, Myctophidae, Melamphaidae) whilst current evidence indicates that their bathypelagic counterparts tend to have demersal relatives (e.g. Alepocephalidae). Pelagic members of additional demersal families, such as *Brotulataenia* spp. (Cohen, 1974) & *Thalassobathia pelagica* (Cohen, 1963) (Ophidiidae); *Sciadonus* spp. (Nielsen, 1969) (Aphyonidae); *Odontomacrurus murrayi, Macrouroides inflaticeps* and *Squalogadus modificatus* (Marshall, 1973), *Mesobius berryi* and *Nezumia parini* (Hubbs & Iwamoto, 1977) (Macrouridae), could possibly compliment this list when further distributional evidence is obtained.

-2. Facultative pseudoceanic species are identifiable as a normally oceanic group whose members adopt a self-maintaining pseudoceanic distribution beyond their normal geographic limits. *Benthosema glaciale* is an example. According to Nafpaktitis et al.(1977) it is the top ranking myctophid of the subpolar-temperate region of the North Atlantic, yet its disjunct distribution shows it also to be abundant in the Mauretanian upwelling area. In examining this distribution further, Badcock (1981) showed that *B.glaciale* has its centre of distribution over the slope where it breeds and thrives. Badcock (1981) noted five other species (viz: *Stomias boa, Notolepis rissoi, Myctophum punctatum, Symbolophorus veranyi* and

Table I Examples of obligatory pseudoceanic species

FAMILY	SPECIES	SOURCE
MESOPELAGIC:		
Gonostomatidae	*Triplophos hemingi* *	Gray,1964
Sternoptychidae	*Maurolicus muelleri*	Mukhacheva,1981
	Argyropelecus gigas	Badcock pers.comm.
	Polyipnus spp.	Baird,1971
Photichthyidae	*Polymetme corythaeola* *	Grey,1964
	Yarella blackfordi *	Grey,1964
Alepocephalidae	*Xenodermichthys copei* *	Krefft,1985 IOS unpubl. data
Notosudidae	*Scopelosaurus* spp*	Bertelsen et al.,1976
Myctophidae	*Diaphus garmani, D.minax, D.roei* *, *D. taaningi*	Nafpaktitis et al.,1977
	Diaphus coeruleus *	Nafpaktitis,1978
	*Diaphus adenomus**, *D.gigas D.sagamiensis, D.suborbitalis, D.watasei* *	Kawaguchi & Shimizu, 1978
	Diaphus dumerili	Gjosaeter & Kawaguchi,1980
	Lampadena pontifix	Hulley,1981
	Lampanyctodes hectoris	Hulley,1981
Zoarcidae	*Melanostigma atlanticum**	Markle & Wenner,1979; Merrett et al. 1986
Melamphaidae	*Melamphaes acanthomus*	Ebeling, 1962
BATHYPELAGIC:		
Alepocephalidae	*Bajacalifornia megalops* *	Krefft,1985
	Bathytroctes microlepis *	Krefft,1985
	Photostylus pycnopterus	Wisner,1977
	Xenodermichthys copei *	Nybelin,1948; Markle & Wenner, 1979; Krefft, 1985, IOS unpubl. data
Zoarcidae	*Melanostigma atlanticum**	Cohen & Pawson,1977
	Parabrotula plagiophthalmus	IOS unpubl. data

* Species exhibiting some dependence on the sea-floor.

Notoscopelus bolini) with similar populations in this upwelling area, apparently isolated from northerly and Mediterranean ones.

It is noteworthy here that pseudoceanic distributions may appear misleadingly complex without reference to broad scale topographical features. Thus many such species inhabit island locations and numerous rises and ridges with steep slopes at bathyal depths (200-2000m) which are separated from continents by expanses of oceanic floor (i.e. the thalassobathyal zone of Andriashev, 1977 and see Parin, 1984 and this volume); areas where enriched productivity may also occur (cf. Isaacs & Schwartzlose, 1965).

More detailed examination reveals further patterns among pelagic slope-dwelling fishes:

- 1. Variation in relative density.

a Obligatory pseudoceanic species are often numerical dominants among pelagic slope populations. *Maurolicus muelleri* is a panoceanic example of a species frequently dominant in density of occurrence (Gjosaeter & Kawaguchi, 1980)(Table II). Indeed, in upwelling areas obligatory pseudoceanic species may occur in exploitable quantities. *Lampanyctodes hectoris*, for example, was the major component of the South African lanternfish catch of 42,560 tons during 1969-73 (Hulley, 1981).

b Facultative pseudoceanic species are found in increasing density in the up-slope direction. Badcock (1981, Table 7) demonstrated an increase in density of almost two orders of magnitude in *Benthosema glaciale* among samples (0-500m depth) over the sounding range 3010 - 100m.

c Certain oceanic species abutting the slope evidently occur in greater densities in slope regions. *Notoscopelus elongatus kroeyeri*, for instance, has a sub-polar temperate distribution according to Nafpaktitus et al. (1977). It is abundant to the west of the British Isles (Gjosaeter & Kawaguchi, 1980). Yet recent preliminary investigations of the near-bottom ichthyofauna of the Rockall Trough in this same area of the eastern North Atlantic to the west of Britain, using commercial sized midwater and demersal trawls by the Institut für Seefischerei, Hamburg, showed mesopelagic densities of *N.e.kroeyeri* three orders of magnitude larger over the slope than in the middle of the Trough (Merrett et al., 1986)(see Table II).

The influence on the vertical distribution of oceanic species caused by the slope intercepting their preferred range is poorly known. Bailey (1982) has indicated that blue whiting, *Micromesistius poutassou*, take up a demersal habit as the slope crosses their usual depth of occurrence (300-500m). Among decapod crustaceans, however, Hargreaves (1984) has shown that some, but not all, mesopelagic species may shift their vertical distribution under the influence of the slope and may increase in abundance close to the sea-floor. Bathypelagic decapod crustaceans appear to be unaffected.

-2. Maximum body size attained by mesopelagic pseudoceanic species is often greater than among their pelagic congeners. According to Kawaguchi & Shimizu (1978) 'most of the slope water [*Diaphus*] species grow larger than the oceanic water species and sometimes reach 20cm or more'. Indeed, *D.watasei* and *D.coeruleus* attain 150-300mm and are among the largest myctophids known (Gjosaeter & Kawaguchi, 1980). Among the sternoptychids, the pseudoceanic *Argyropelicus gigas* attains greatest individual size (120+mm SL); while *Yarella blackfordi* (300+mm SL) and *Polymetme corythaeola* (200+mm SL) are among the largest photichthyids known, as is *Triplophos hemingi* (350+mm SL) among the gonostomatids. Conversely, none of the recognized bathypelagic pseudoceanic species attain larger size than their oceanic congeners.

RESEARCH APPROACHES

While endemism has been demonstrated among pelagic as well as demersal slope-dwellers, the details of congruency of the various faunal elements need further investigation. To facilitate this end, it is worthwhile considering the value and limitations of the diversity of approach employed hitherto.

DIRECT APPROACHES

a Nets

1. A variety of midwater trawls have provided the basic information on the biogeography of pseudoceanic species (e.g. conical ring nets - Kawaguchi & Shimizu, 1978; Isaacs-Kidd midwater trawls IKMT- Jahn & Backus, 1976; Nafpaktitus et al., 1977; mouth opening/closing rectangular midwater trawls (RMT 1+8) - Badcock, 1981; commercial-sized gear - Krefft, 1974; Gjosaeter, 1984; including information on the occurrence of benthopelagic fish far above the sea-floor -Haedrich, 1974; Krefft, 1980; Stein, 1985; I.O.S. unpubl. data). Obviously mouth opening/closing devices greatly enhance the value of net collection data and their use is increasing.

2. Demersal trawls have also contributed to the knowledge of pseudoceanic species (e.g. *Yarella* spp., *Polymetme* spp. and *Triplophos hemingi* - Grey, 1964; *Scopelosaurus* spp. - Bertelsen et al. 1976; *Diaphus coeruleus*

Table II Ranked abundance of the more numerous fish species (>3%) in demersal (200BT) and pelagic (1600PT) trawl samples from the slope and middle of the Rockall Trough.

SOUNDING/ DEPTH RANGE (M)	SLOPE (east and west combined) 200 BT SPECIES	%	1600 PT SPECIES	%	MID TROUGH 1600 PT SPECIES	%
100					(n=443)	
					Maurolicus muelleri	48.8
					Benthosema glaciale	28.4
					Argyropelecus hemigymnus	7.7
					Argyropelecus olfersi	4.1
					Notoscopelus kroeyeri	3.8
190-220*	(n=13,638)		(n=102)			
	Micromesistius poutassou	42.7	*Maurolicus muelleri*	50.0		
	* *Gadiculus argenteus thori*	35.2	*Micromesistius poutassou*	48.6		
	Melanogrammus aeglefinus	10.1				
	* *Helicolenus dactlyopterus*	8.2				
280-318*	(n=228)		(n=8461)			
	Micromesistius poutassou	64.0	*Notoscopelus kroeyeri*	50.4		
	* *Lepidorhombus whiffiagonus*	8.8	*Micromesistius poutassou*	39.8		
	Helicolenus dactylopterus	6.1	*Benthosema glaciale*	6.5		
	* *Molva molva*	3.1				
	* *Malacocephalus laevis*	3.1				
397-414*	(n=563)		(n=9439)		(n=416)	
	Micromesistius poutassou	49.6	*Notoscopelus kroeyeri*	82.8	*Benthosema glaciale*	23.3
	* *Chimaera monstrosa*	11.8	*Micromesistius poutassou*	11.1	*Lampanyctus crocodilus*	20.4
	* *Glyptocephalus cynoglossus*	7.7	*Benthosema glaciale*	4.6	*Stomias boa ferox*	11.3
	Lepidorhombus whiffiagonus	4.6			*Lobianchia gemellari*	9.1
	* *Molva molva*	3.2			*Chauliodus sloani*	3.6
	* *Helicolenus dactylopterus*	3.1			*Xenodermichthys copei*	3.6
					Sagamichthys schnakenbecki	3.1

	(n=506)		(n=1732)			
	* *Chimaera monstrosa*	48.3	*Notoscopelus kroeyeri*	24.2		
	* *Lepidion eques*	22.1	*Lampanyctus crocodilus*	15.6		
	* *Helicolenus dactylopterus*	4.7	* *Halargyreus johnsoni* (juvs)	12.5		
	* *Glyptocephalus cynoglossus*	4.7	*Stomias boa ferox*	8.7		
598-637	* *Epigonus telescopus*	4.5	*Myctophum punctatum*	6.9		
	* *Molva dypterygia*	3.2	*Benthosema glaciale*	5.7		
			Melanostigma atlanticum	5.1		
			Xenodermichthys copei	3.7		
			Lobianchia gemellari	3.3		
					(n=989)	
					Maurolicus muelleri	52.6
700					*Scopelogadus beanii*	10.4
					Lampanyctus macdonaldi	7.3
					Benthosema glaciale	6.6
					Lampanyctus crocodilus	4.4
					Normichthys operosus	3.2
	(n=640)		(n=965)			
	* *Coryphaenoides rupestris*	36.0	*Melanostigma atlanticum*	32.8		
	* *Lepidion eques*	11.3	*Notoscopelus kroeyeri*	18.1		
	* *Nezumia aequalis*	10.1	*Benthosema glaciale*	9.4		
794-841	* *Galeus melastomus*	8.2	* *Synaphobranchus kaupi* (juvs)	7.8		
	* *Aphanopus carbo*	5.2	*Lampanyctus crocodilus*	3.5		
	* *Alepocephalus bairdii*	5.0	* *Coryphaenoides rupestris*	3.2		
	* *Glyptocephalus cynoglossus*	3.6				
	(n=1401)				(n=539)	
	* *Alepocephalus bairdii*	51.7			*Lampanyctus macdonaldi*	28.0
	* *Coryphaenoides rupestris*	20.2			*Scopelogadus beanii*	15.6
	* *Aphanopus carbo*	4.4			*Lampanyctus crocodilus*	10.6
	* *Halargyreus johnsoni*	3.9			*Benthosema glaciale*	6.7
	* *Lepidion eques*	3.2			*Normichthys operosus*	5.9
	* *Trachyrincus murrayi*	3.1			*Stomias boa ferox*	4.8
	* *Nezumia aequalis*	3.0			*Chauliodus sloani*	3.3
					Bathylagus euryops (dark)	3.2
					Lobianchia gemellari	3.0

and *D. watasei* -Nafpaktitis, 1978). The generally large size of these demersal specimens of both the latter species was remarked upon by Nafpaktitis et al.(1977).

3. Near bottom sampling is improving our knowledge of the congruency of the pelagic and demersal slope ichthyofauna. For example, initial trials of a near-bottom echo-sounder integrated with the I.O.S. net monitor for use with the RMT 1+8 have already given promising results. While this gear samples micronekton, the recent preliminary investigations of the slopes of the Rockall Trough, mentioned above, sampled a much larger size spectrum with a midwater trawl of mouth opening 30m x 20m high and a bottom trawl of 22m x 6m headline height. (Merrett et al., 1986).

Over a five day period, eleven demersal hauls were taken from both sides of the Trough at approximately 200m intervals from 200-1000m soundings, and nine midwater hauls from similar localities were fished with the footrope 0-10m (1 tow), 3-18m (7 tows) and 60m (1 tow) above the seabed. In addition four mid-Trough samples were taken (100,400, 700 and 1000m depth) over 2550-2620m soundings. The total collection yielded some 40,000 fish (23,000 mesopelagic and 17,000 demersal) belonging to 108 species. Nineteen species were peculiar to the mid-Trough catches and only 27 were common to both pelagic and benthic gears. However, only 38 species comprised >3% of the catch in any one sample. The only mesopelagic species to be ranked among demersal catches was *Micromesistius poutassou*, which is consistent with its known tendency to impinge on the slope as this traverses its depth distribution (Bailey, 1982). Only in pelagic tows over the slope were demersal species (3) present in sufficient proportion to warrant inclusion, despite the close proximity to the bottom of the pelagic trawl (Table II). This is the first substantial observation, despite obvious sampling limitations, that the bulk of the demersal and pelagic fish populations remain separate over the slope, with the former evidently swimming in layers very close to the bottom.

b Submersibles.

Reports of pelagic oceanic fishes observed close to the sea-bed are scarce, but valuable. Cohen & Pawson (1977) observed the pseudoceanic zoarcid, *Melanostigma atlanticum*, at 1960m, while Nafpaktitis et al., (1977) remark on large *Lampanyctus macdonaldi* swimming very near the bottom.

INDIRECT APPROACHES

a Feeding studies

Demersal slope fishes have provided considerable data on the occurrence of pelagic oceanic species in stomach contents. Assuming that most, at least, were alive when eaten, and the condition of many seen personally suggest it, this is a useful means of assessing near-bottom faunal interaction. For instance, a less than exhaustive examination of the literature on Atlantic collections revealed 34 species representing 18 families (14 bentho-pelagic and 4 benthic) of demersal fishes containing identifiable remains of 24 species from 10 families of meso-and bathypelagic fishes.

b Parasite 'tags'.

Merkle & Wenner (1979) demonstrated the dependence on the sea-bed of *Melanostigma atlanticum* from a knowledge of its reproductive biology and temporal changes in its endoparasitic fauna. The value of such parasite 'tags', both internal and external, was further discussed by Campbell et al., (1980). The implications that the parasite infection rate among demersal fish > mesopelagic fishes > bathypelagic fish in the current context are obviously interesting.

c Eggs and larvae

Studies of eggs and larvae offer another worthwile perspective of research. Data are sparse, but work on *Lampanyctodes hectoris* from off southwest Africa and New Zealand has identified eggs and larval stages and shown that both occur over the outer shelf and slope in 14-15°C water after spring spawning (Ahlstrom et al., 1976; Robertson, 1977). The distinctive eggs of *Maurolicus muelleri* are well known. In the North Atlantic and off New Zealand they are spring-summer spawners with eggs and larvae occupying 100-500m levels and temperatures of 8-22°C (Williams & Hart, 1974; Robertson, 1976). Off Japan Okiyama (1971) observed the majority of eggs in the surface layers (0-50m), with few larvae above 75m depth. In all three examples distribution was centred over slope waters, though the North Atlantic observations were from the thalossobathyal fauna. Hamann et al.,(1981) investigated hydrographic effects on larval distribution in the Mauretanian upwelling area and found highest concentrations over the slope with good correlation between *Myctophum punctatum* larvae and water masses (cf. above). Conversely, ontogenetic descent from the surface waters of the pelagic larvae of demersal species *Coryphaenoides* spp. has been demonstrated from RMT 1 + 8 collections (Merrett, 1978). Extension of the above studies to investigate reproductive patterns would also be beneficial.

d Diet and morphological variation

Clarke (1984) postulated the separation of two sexually dimorphic species of snipefish previously recognised as *Macrorhamphosus scolopax* on these criteria.

Thus, while improved sampling techniques and increased effort are necessary to elucidate many of the complexities of biogeographical congruence around the oceanic rim, a variety of ecological pointers are also available to complement this endeavour substantially.

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MONSOON REGIME IN THE INDIAN OCEAN AND ZOOPLANKTON VARIABILITY

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INTRODUCTION

The effect of the monsoon in the Indian Ocean is limited to north of 10°S, the area being defined as the region of seasonally changing monsoon gyre (Wyrtki, 1973). The southwest monsoon (SW) is prevalent from May to September when the cyclonic circulation in the surface waters of the Arabian Sea and Bay of Bengal results in water movement from west to east. The wind direction is reversed during the northeast monsoon (NE) period extending from November to March and the gyre becomes anticyclonic leading to a circulation from east to west. The monsoonal effects on zooplankton lead to characteristic zoogeographic patterns in the open ocean and coastal waters.

Studies of zooplankton variability were taken up since the International Indian Ocean Expedition (1960-65) and later surveys made by the National Institute of Oceanography (Rao, 1979; Rao et al.,1981). The various aspects presented here are based mainly on the author's investigations covering a period of about fifteen years. The evaluation is presented in three sections to show how the monsoon exerts its influence on zooplankton from different types of environment.

OPEN OCEAN

The reversal of the monsoon circulation is one of the most important factors affecting the abundance and diversity of zooplankton in the open ocean and is reflected in the relative abundance of total zooplankton biomass (IOBC, 1968) and common groups like copepods (IOBC, 1970), chaetognaths (Nair, 1972), pelagic tunicates (Nair & Iyer, 1974), decapod larvae (IOBC, 1970), pelagic molluscs (IOBC, 1971) and others. This is true whether the entire group or a species belonging to the group is concerned. Higher abundance of the group/species is observed along the north eastern part of the Indian Ocean (Bay of Bengal) during the SW monsoon, when the circulation is from west to east. During the NE monsoon period, the flow is reversed and the relatively higher population existing in the eastern side begins to spread along the west coast of the Indian peninsula. This is well marked in the zoogeography of *Sagitta bedoti, S.bipunctata, S.enflata, S.pacifica, S.regularis* and *S. robusta* (Nair, 1972; 1977)(Table I).

On the western side of the Arabian Sea, as a result of its reversal, the Somali current transports zooplankton meridionally across the equator both in southern and in northern directions according to the time of year. The samples collected during the Lusiad Expedition in July/September 1962, along the equatorial region of the Indian Ocean with north-south transects covering the equatorial Current System show this (Nair, 1976). Common groups and different species of chaetognaths reach maximum population density west of 57°E, suggesting a meridional distribution on the western side and a zonal distribution along the remaining part of the equatorial zone (Fig. 1). Upwelling enriches the Somali waters during the SW monsoon period and the current carries part of the dense population seen off Somalia towards the eastern part.

COASTAL WATERS

The coastal waters of the tropics are highly productive and sustain a rich and abundant plankton life. This area is also influenced by the seasonal variations in rainfall on account of the monsoon. Here the monsoonal effect is more during the SW monsoon (June to November) when freshwater influx from rivers and estuaries

Table I Average number of different species in the Arabian Sea with average numerical values of the selected 5° squares.

Species	AREA 1 (10-15°N & 50-55°E)			AREA 2 (20-25°N & 65-70°E)			AREA 3 (15-20°N & 70-75°E)			AREA 4 (5-10°N & 75-80°E)		
	NE	SW	TOTAL	NE	SW	TOTAL	NE	SW	TOTAL	NE	SW	TOTAL
K.pacifica	27.86	11.15	39.01	13.45	14.50	27.95	31.24"	43.20'	74.44	22.53	32.70	55.23
K.subtilis	2.61	21.99'	24.60	1.62	-.—	1.62	1.00	-.—	1.00	12.53"	5.28	17.81
Pt.draco	116.26	78.90	195.17	3.54	6.50	10.04	58.61	30.70	89.31	130.88"	180.07	310.95
S.bedoti	381.90"	215.94	597.84	116.51	31.30	147.81	75.06	21.05	96.11	232.78	505.37	738.15
S.bipunctata	76.09	84.28'	160.37	75.71	9.80	85.51	168.23"	22.70	190.93	80.90	19.85	100.75
S.enflata	1865.47"	1423.34	3288.81	682.77	211.40	894.17	905.43	416.75	1322.18	1315.37	2520.28'	3835.65
S.ferox	2.89	26.07	28.96	0.14	8.20	8.34"	5.66	23.80	29.46	8.92"	4.43	13.35
S.hexaptera	17.26"	17.92	35.18	0.24	0.10	0.34	4.20	1.00	5.20	12.69	19.85'	32.54
S.minima	4.44"	12.92'	17.36	0.10	-.—	0.10	-.—	-.—	-.—	1.08	-.—	1.08
S.neglecta	8.94	65.29	74.23	94.74"	11.40	106.14	10.66	15.10	25.76	32.53	75.97'	108.50
S.pacifica	164.78	274.23	439.01	62.50	19.10	81.90	190.00"	18.95	208.95	184.41	425.54'	609.95
S.pulchra	21.65"	22.45	44.10	11.97	0.30	12.27	2.53	3.30	5.83	9.38	27.85'	37.23
S.regularis	67.60	71.82	139.42	1.96	18.10	20.06	146.45"	25.00	171.45	47.22	150.23'	197.45
S.robusta	98.68"	84.82	183.50	7.71	4.50	12.21	17.38	1.85	19.23	8.69	86.11'	94.80
TOTAL	2856.54	2411.12	5267.66	1072.96	343.70	1416.66	1617.91	623.40	2241.31	2108.11	4053.53'	6161.64

' Maximum observed value during the SW monsoon period

" Maximum observed value during the NE monsoon period

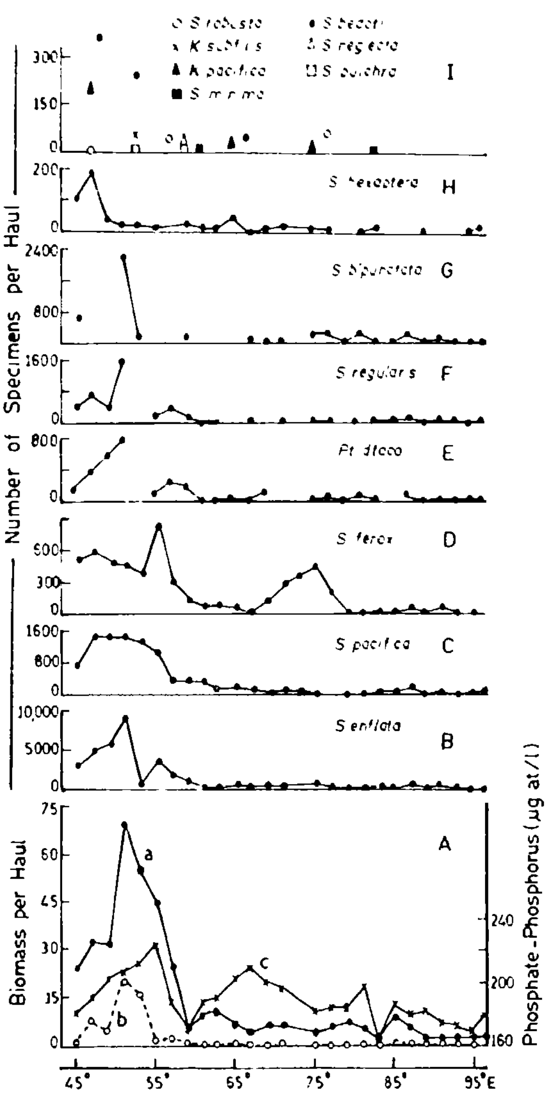

Fig.1 Distribution of (A) total zooplankton, chaetognath volume, phosphate phosphorus and (B to I) different species of Chaetognaths along the equatorial east-west transect of the Lusiad Expedition in the Indian Ocean (a, total zooplankton: b, chaetognath volume and c, phosphate phosphorus).

lower the salinity along the coast to 30-34.5⁰/oo.

In general, throughout the Indian coastal waters the annual zooplankton distribution is bimodal with two peaks - one just before the monsoon and the other just after the rain. (Rao, 1979, Rao et al.,1983). The plankton production triggered during the SW monsoon period (June - September) makes the region an excellent pasturage for the plankton feeders and in general, the peak fishing season along the coastal waters coincides with this period (Nair, 1982).

Along the east coast there is an increase in the biomass of zooplankton from north to south whereas a reverse pattern has been observed during October to November along the west coast (Nair, 1977). The incidence of high densities of chaetognaths along the two coasts also follows a similar pattern. Along the west coast, off Bombay the population maximum of chaetognaths was seen in November-December (Nair et al., 1981), south of Bombay, off Calicut in October - November and further south at Trivandrum the peak observed was much earlier (July - September). On the east coast, the peak periods for the chaetognath species were found off Madras during May - August, and towards the South in the Gulf of Manner it was in November and December (Rao et al., 1981). The prevailing difference in salinity, periods of upwelling and surface currents may contribute to this pattern of abundance. Upwelling along the west coast starts in March and continues during the SW monsoon with its maximum effect in August - September. It sets in earlier in the south and gradually extends to the north (Rao, 1979) and concomitant with this, the movement of peak zooplankton abundance is also from south to north.

ESTUARIES

The monsoon exerts stress on estuarine fauna by bringing about a drastic change in salinity, which was more marked towards the upper reaches. During the high salinity period zooplankton maintained a high level of production of about 3 to 7.5 times that of the relatively low standing stock of zooplankton observed during the low salinity period (Nair, 1982).

The low saline fauna replacing the high saline species are not at all diverse or rich in comparison (Rao et al., 1981). Neritic species like *Sagitta bedoti* penetrate to the upper reaches of the estuarine system during the premonsoon period when a uniform salinity (25.3

- 33.5°/oo) prevailed throughout the system (Nair, 1974). In the postmonsoon period the chaetognath population synchronically followed the steep gradient in salinity (0.2 to 28.6°/oo) along the estuary and became restricted to its seaward end.

CONCLUDING REMARKS

In the open ocean the semi annually reversing system of currents exert profound influence on the shifting of zooplankton populations. The assumption is based on samples mostly collected from the upper 200m of the Indian Ocean and the limit of such influence is yet to be ascertained. In the coastal waters the time lag involved in the north to south or reverse pattern of movement of species along with associated factors responsible for such variability calls for detailed investigation. Estuaries with the characteristic fluctuations in salinity on account of monsoon and the theory of repopulation are aspects to be studied in detail.

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MODELS AND PROSPECTS OF HISTORICAL BIOGEOGRAPHY

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The distribution of organisms may be considered from various points of view, which reduce to two: ecology and systematics. Each has a history of about 200 years, the former beginning with Humboldt, the latter with Candolle (Nelson, 1978; Browne, 1983). Ecology sees causal explanation in measurable factors of the environment - elevation, temperature, latitude, depth, salinity, etc. Systematics sees it in historical circumstance - in evolution in some sense - because the ecologic factors, even in their totality, are always insufficient. A species rarely, if ever, lives everywhere that is ecologically suitable.

I focus on the systematic aspect. How do we discover historical circumstance and acquire the knowledge needed for satisfactory explanation? Traditionally it was hoped that this knowledge would emerge from study of the fossil record. This has proved a vain hope, not merely because the fossil record is incomplete, but because data of the record do not contain the knowledge. To overcome this deficiency fossils were often viewed as ancestors of recent taxa. This presumed relationship, read into the data of the record, was sometimes, and sometimes still is, believed crucial evidence of historical circumstance. But this belief, in crucial evidence, has also proved vain. Ancestors and their geographic analogs - centers of origin - are not empirical entities that await discovery (Nelson, 1983a). Rather, they are constructs - one might even term them artifacts - arising from a particular view of systematics (Nelson & Platnick, 1984a). These vanities have become clear to many persons for many reasons. Cladistic systematics is one attempt to remedy the problem (Eldredge & Cracraft, 1980; Funk & Brooks, 1981; Wiley, 1981; Platnick & Funk, 1983). Panbiogeography is another (Croizat, 1958, 1964). Vicariance biogeography is an attempt, for better or worse, to marry the two (Nelson & Rosen, 1981; Nelson & Platnick, 1981). These attempts may also prove vain, but at the moment not yet (Patterson, 1983).

An element common to these attempts is to vizualize systematic relationships not in terms of fossil ancestors and living descendents but as descendants only. This view is not problematic, for all ancestors are also descendents. Viewed as such they differ only in degree of relationship.

Thus taxa 3 and 4 (Fig. 1) may be viewed as related to each other more closely than to taxa 1 and 2. Such is true even if 3 is the ancestor of 4, or vice versa; or if 1 is the ancestor of 2, or 2 of 3, or whatever. Geographically the idea is that the relationships of taxa might indicate the historical relationships of the geographic areas. If so, areas C and D are related to each other more closely than to areas A and B, according to the evidence of the interrelationships of taxa 1-4, where taxon 1 occurs in area A, taxon 2 in area B, etc. However simple to understand, this model is not a description of biological distribution as we find it. The model merely illustrates a particular notion of area relationship. This notion is important, for

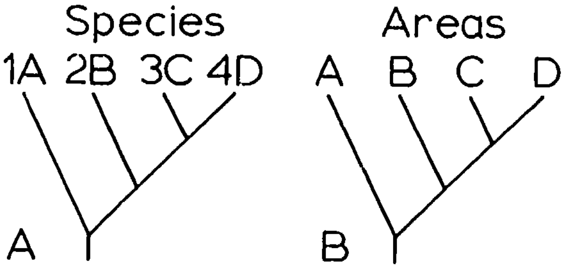

Fig. 1 A: Cladogram of four taxa (species 1-4) in four areas (A-D). B: Corresponding area cladogram (after Nelson, 1982, Fig. 1).

it is the basis for the analytical procedures of cladistics and vicariance.

A different notion is based on similarity of biota. As an example I mention an analysis of the distribution of cowries, genus *Cypraea* , occurring in four areas: Japan, Philippines, New Caledonia, Queensland (Nelson, 1984a). If we count the species common to pairs of areas, the Philippines and Quyeensland have the highest number. We might believe that these areas are related on this evidence -- the high number of taxa common to them. If so, we would have a different notion of area relationship, which is independent of any cladistic information.

Yet another notion is that formalized by Hennig (1966): the progression rule. Geographic distributions are treated as characters, and distributions are assigned to hypothetical ancestors, so as to minimize dispersals (Nelson, 1969; Nelson & Platnick, 1984b). Interestingly, most of the clues, or rules, historically used to determine a center of origin, reduce to this formalization, which is constrained by cladistic information (Platnick, 1981). Unfortunately, the progression rule is biased so as always to resolve a center of origin, even when no center of origin need have existed (Nelson, 1975).

Vicariance biogeography attempts to focus on the cladistic information, in the hope that this information, when cast geographically, will have validity across taxa, and across the gulf that separates biological evolutaion from geological evolution. In this regard vicariance takes inspiration from Croizat, who tirelessly stressed that earth and life evolve together; that life is but the superficial layer of the rocks; that taxonomic differentiation is life's response to a dynamic geology.

These slogans are imbued with the wishful thought, which Croizat stressed as empirical fact, that life is tightly bound to, and ordered by, the earth's tectonic history. Croizat did not deal with pelagic distribution, which is complicated by a second level of tectonics - the structured water-masses, the boundaries of which frequently limit the geography of taxa. The processes at the geotectonic level ultimately determine events at the hydrotectonic level, and perhaps the relation is firmly deterministic. On the other hand, the two levels may be largely decoupled. If so, the history of pelagic distribution may forever be elusive to a vicariant interpretation.

If we turn to geotectonics we find conflicting views. In contrast to the classic drift theory, earth expansion holds that the modern Pacific Basin began, as did the Atlantic and Indian Basins, by continental rifting in Mesozoic time (Carey, 1976, 1983). A kind of hybrid theory, of "Pacifica", holds, as does the classic view, that the Pacific is the oldest ocean, but that it contained a continental mass that rifted into fragments, which eventually dispersed around the modern basin (Nur & Ben-Avraham, 1978). In support of these views is the known age structure of the world sea floor - about the same in all three ocean basins (Pitman et al., 1974).

These are themes relevant to Croizat's synthesis of terrestrial distribution, in which there is symmetry of transoceanic relationship across all three basins. In addition there are boreal and Antarctic patterns, making a total of five major types of distribution.

These are themes relevant to pelagic biogeography, for the question here is the relative age of origin of the deep ocean basins and the open-water habitat. If the distribution of pelagic organisms reflects anything of history, why not the history of the basins? So, what are the patterns? and to what history do they testify?

My approach is not through the study of pelagic distribution, but through a particular family of fishes, Engraulidae (anchovies). Of some 150 species, there is perhaps one that has a pelagic, rather than inshore or freshwater, habit. It is widely distributed throughout the Indian and West-Central Pacific Oceans, and it has the most widespread distribution of any anchovy. Perhaps it evidences the decoupling of the pelagic from the shelf, yet the species, *Encrasicholina punctifer* = *Stolephorus bucccaneeri* , is not ubiquitous in tropical oceans. Its eastern limit is the East Pacific Barrier; and its western, the Cape of Good Hope; in these respects it is not unusual.

Anchovies are interesting because they show much the same, apparently trans-Pacific, relationship as many marine groups, including the Spanish mackerels (Collette & Russo, 1985), and the epipelagic sergestid crustacean *Acetes*

(Omori, 1975), which is differentiated in the New World along both coasts of the Americas and in South American freshwater as well. Anchovies do much the same but on a grander scale. Some 70 species are involved in the New World differentiation, with more than 20 of them confined to South American freshwater, which is unique in this respect. There are few, if any, freshwater anchovies elsewhere. The details of relationship seem to confirm, and possibly extend, the notion of interocean connection (Van der Spoel, 1983; Van der Spoel & Heyman, 1983).

The trans-Pacific character of this distribution was not clear, for the traditional taxonomy of the group broke into Old World and New World sections. Cladistic analysis of the group associated some Old World forms (from the West and Central Pacific) with those of the New, and the trans-Pacific character became evident. Interestingly, the West-Central Pacific section is a small one, with only five species (one endemic in Hawaii), in contrast with the New World section, with a relatively massive radiation in the tropics, involving a dozen or more species sympatric, and typically collected together, in areas like the Gulf of Panama (Hildebrand, 1943; Nelson, 1983b).

Seemingly anomalous, and embedded in this trans-Pacific distribution, is the genus *Engraulis*, a world-wide genus with temperate representatives in areas of classic concern (Nelson, 1985), occurring there with sardines and other epipelagic organisms (Hedgpeth, 1957).

Bipolarity, or antitropicality, is interesting. There are two reviews of note (Ekman, 1935; Du Rietz, 1940). Here the Pacific Basin is relevant, for the distributions of individual taxa, when considered together, outline the Pacific Basin fairly exactly, be the taxa terrestrial plants or marine animals. So we are led to ask if bipolarity is a reflection of the development of the Pacific Basin. Anchovies testify that such is the case.

As revealed by sea-floor spreading data, the Pacific is unique in its extensive north-south spreading, as reflected particularly in the Pacifica model. The basin expands radially, in contrast to the other basins, which expand laterally. I do not claim that anchovies prove the Pacifica model, or earth expansion, but they seem an example of a group differentiated in response to a growing rather than shrinking Pacific Basin. And they illustrate a vicariant approach to biological distribution that if not truly pelagic, at least borders on being so.

Anchovies are interesting because their terminal differentiation is bound with the Pliocene closure of the Panamanian Isthmus, suggesting a progressively older history for the South American freshwater, the bipolar (antitropical), and the trans-Pacific patterns (Nelson, 1984b). But how old?

A review of the fossil anchovies (Grande & Nelson, 1985) was not much help, but showed that the oldest, from the Upper Miocene of Cyprus, is very similar to the Mediterranean anchovy of today. The group most closely related to anchovies, the herring family Clupeidae, is known from abundant fossil remains from the beginning of the Tertiary. If this relationship is correct, then anchovies are older still, even though their fossil record is very meager.

Even with few fossils, and from them no information not already supplied by recent species, modern taxa and the distributions of anchovies and many other groups are ample, on a world-wide basis, and promise to be richly informative. The key to the systematic information - knowledge of the interrelationships of the species-level taxa (and of the supraspecific groups) - is the promise of cladistics. Suffice it to say that enough progress has been achieved, with anchovies and other groups of plants and animals, to justify an optimistic outlook for the future.

There is a historical factor inherent in geographic distribution, in the pelagic as elsewhere. At present it is largely confounded with variation properly termed ecologic, and our notions of ecology are, as a result, overextended and on occasion whimsical. Surely it would be better if this historical factor could be identified and isolated. It is time that this task be taken seriously, not only by systematics (who do the work) but also by ecologists (who profit from it).

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TRANSITION ZONES AND FAUNAL BOUNDARIES IN RELATIONSHIP TO PHYSICAL PROPERTIES OF THE OCEAN

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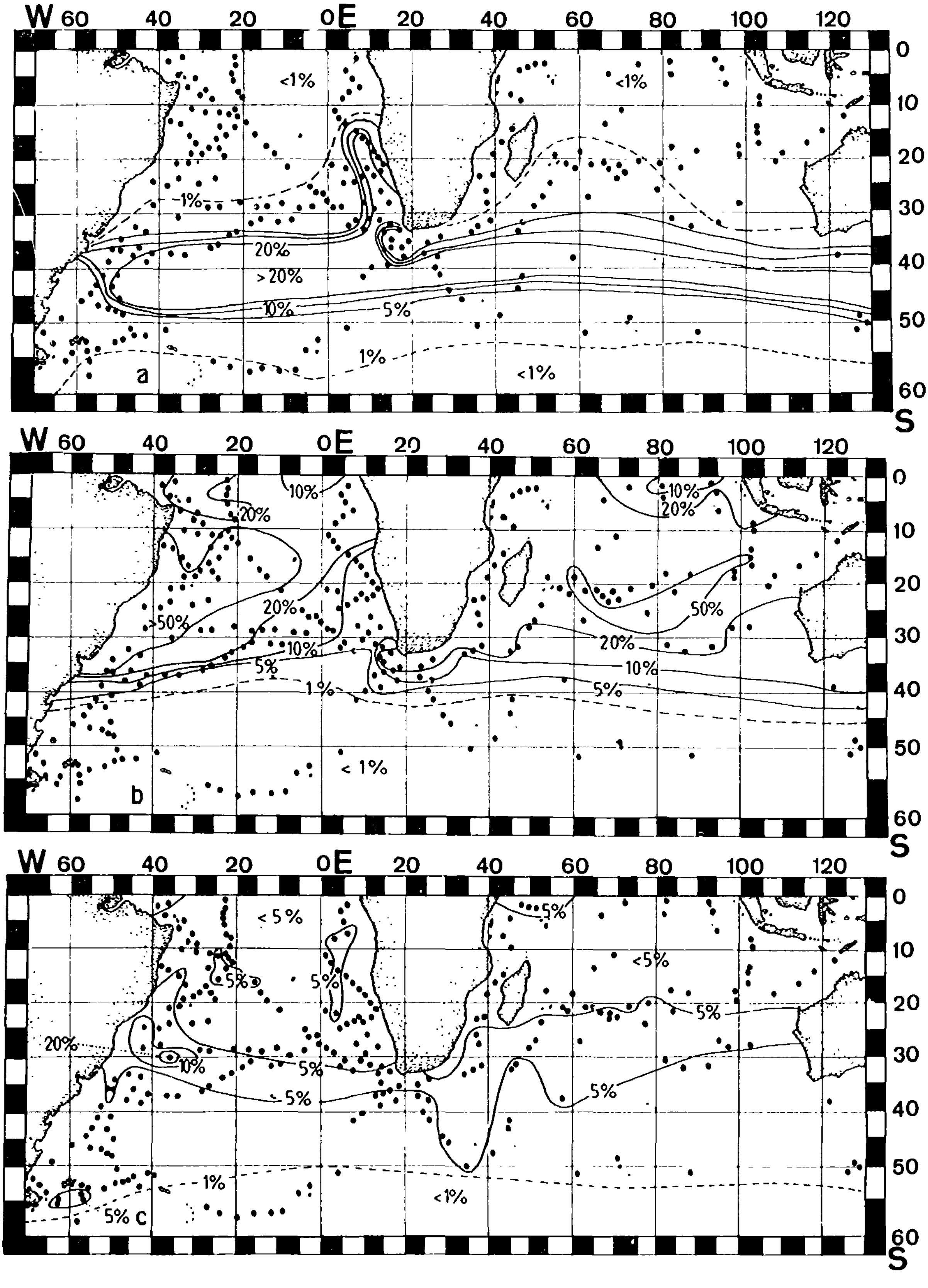
INTRODUCTION

Transition zones are defined in the physical oceanographic literature to be the areas with mixed water mass properties typically associated with boundary current extensions and the boundary between the subtropical gyres and the high latitude circulation systems. In both the physical and biological usage these are finite areas usually differentiated by some hydrographic definition. For example, the North American Slope Water represents a transition zone bound by the 15°C isotherm contour at the 200m surface and the edge of the continental shelf. Biologically, transition zones can be delimited by the range of so-called "transition zone" species and an add-mixture of organisms from both the biogeographic regions bounding the zone. Therefore, translation zones are regions identified by an admixture of properties in both a biological and physical sense. They also contain unique elements in terms of endemic species and in the intense fronts and eddy fields associated with them.

An example of a transition zone in the South Atlantic and southern Indian Oceans as seen in the distribution of planktonic foraminifera is given in figure 1. The distributions of a transition zone species, *Globorotalia inflata* (fig. 1a) ; a subtropical species, *Globigerinoides ruber* (Fig. 1b); and a cosmopolitan species, *Globigerinita glutinata,* (Fig.1c) taken from the work of Bé and Tolderlund (1971) are shown.

Distributions are presented in terms of the abundance relative to the total foraminifera population. The transition zone across the southern edge of the subtropical gyres in these oceans is centered around the extensions of the Brazil and Agulhas currents. The transitional species extend equatorward into the upwelling regime off southwestern Africa which is a pattern found in many faunal forms around the globe. The range of *G. ruber* (fig. 1b) overlaps the transition zone to the center of the compositional maximum of *G. inflata.* Subpolar species such as *G. pachyderma* (not shown) are similarly found in this zone but with a compositional shift to the south. The cosmopolitan *G. glutinata* (Fig. 1c) is spread from the subarctic to the subantarctic but shows a maximum in its contribution to the total foraminifera abundance along the Brazil coast and at the northern edge of the transition zone as it extends across the southern ocean.

The influence of the physical environment upon the distribution of life in the world ocean can be explored by either carefully mapping the distribution of organisms and physical properties throughout the ocean, or by outlining the extent of the regions providing the correct physical and biological conditions for the existence of a species. The first route of drawing an empirical picture of the link between the physical environnment and the geographical distribution of phytoplankton, zooplankton, and nekton is limited by a sampling problem, i.e., the distributions of species within the sea in relation to the physical features of the ocean circulation are not well enough known to get a very complete picture. The alternate approach of determining the physical constraints on the biology based on a catalog of physical aspects of the situation and our knowledge of the influence they have on organisms is also severely limited by gaps in our understanding of the marine ecosystem and the physiology of most marine organisms. In the distributions in figure 1 and most works dividing the ocean into biogeographic provinces, a combined approach is used; faunal zones are delineated along sections but physical properties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of the environment are used to extrapolate over large areas.

DISTRIBUTION OF PROPERTIES ACROSS TRANSITION ZONES

Transition zones represent regions with strong latitudinal changes in water mass properties. Typically this involves a poleward decrease in the temperature (approx. 10°C in 1000km) and salinity (0.5 to 2.0 parts per thousand in 1000km) with an inverse trend towards higher nutrient levels in higher latitudes as shown in figure 2 for the Atlantic. The frontal boundaries also lead to large contrasts in the depths of the mixed layer and its seasonal cycle. This in combination with enhanced vertical exchange of nutrients in frontal zones and the large-scale gradients in the nutrient distributions produces high variability in the abundance and species composition of phytoplankton in these areas.

The spatial gradients in the phytoplankton suggest very sharp boundaries across currents such as the Gulf Stream and the fronts associated with strong eddy features. For an example of this contrast the reader may look at the CZCS (Coastal Zone Color Scanner) images of near surface chlorophyll in Brown et al. (1985).

The contrasts in horizontal structure of phytoplankton communities along with variations in temperature and salinity across frontal zones lead to large variations in higher trophic levels. The sharpness of faunal boundaries in the zooplankton and nekton depend upon the ability of organisms to withstand changes in physical and biological parameters of their environment. In general, organisms with higher tolerances to variations in their environment will be dispersed more widely across frontal zones than those less able to withstand these stresses. A similar pattern is seen within many species in relation to age, with the adults having a larger distribution in space than the viable reproductive range of the species. The level of dispersal in any species depend both on the level of change the organisms can tolerate and the strength of the eddy exchange processes associated with transition zones and the fronts found in them. This leads us to study the characteristics of the circulation in transition zones and the unique horizontal and vertical mixing typical of these regions.

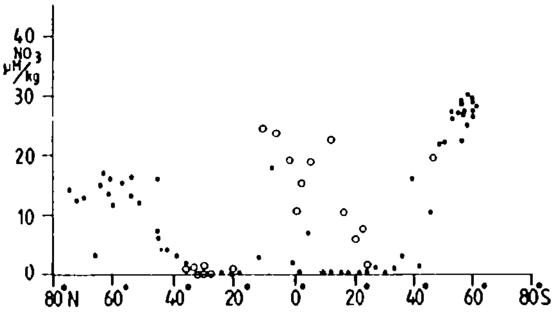

Fig. 2 The concentration of nitrate at a depth of 100m from the Atlantic GEOSECS data set. Dots denote the concentrations on the section down the western basin while the crosses indicate values for the legs in the eastern side of the Atlantic.

ADVECTION/DIFFUSION AND TRANSITION ZONES

In addition to direct responses of organisms to environmental factors such as temperature, salinity, oxygen and nutrient distributions, the inherent motion of water in the world ocean leads to a unique environment. The ocean circulation is a dominant factor in the determination of pelagic distributions. Advection of planktonic organisms by the large-scale ocean circulation coupled with diffusion by turbulent eddy fields plays a role in the establishment of both the reproductive and total range of most species. To consider the influence of advection/diffusion on biogeography compare the mean circulation and eddy field in figure 3 with the distribution of Foraminifera in

Fig. 1 The distribution of three species of foraminifera in the South Atlantic and southern Indian Ocean taken from Be & Tolderlund (1971). Contours are of percent abundance relative to the total forams in the upper 30m of the water column. a) *Globorotalia inflata;* b) *Globigerinoides ruber*, c) *Globigerinita glutinata*.

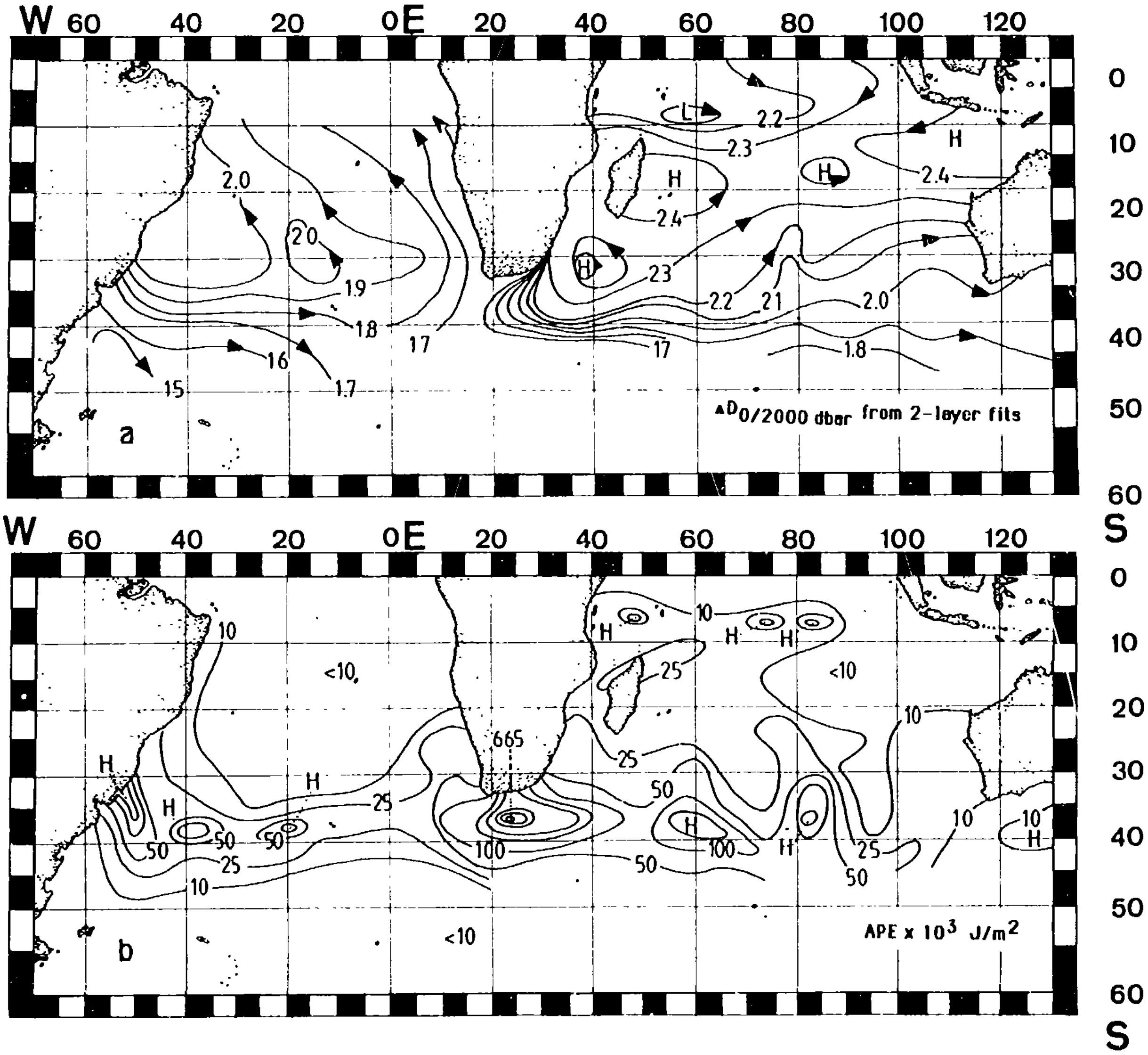

Fig. 3 Dynamic height (a) and eddy available potential energy (APE) (b) for the South Atlantic and Southern Indian Oceans calculated from the U.S. Navy MOODS historical data set with a two-layer diagnostic model. For a detailed description of the computations see Olson et al. (1985)

figure1.

The mean dynamic height field for the surface relative to 2000dbar (Fig. 3a) shows the flow in the subtropical gyres of the South Atlantic and southern Indian Oceans. Comparison with the distribution of the transition species, *Globorotalia inflata*, in figure 1(a) shows the area where this foram composes over 20% of the population; the distribution follows the eastward flows across the poleward edge of both gyres. Although the connection between the two basins is not well represented in figure 3(a) due to the grid spacing and the limitations of the calculation, a portion of the eastward flow in the South Atlantic continues to add to the flow across the southern edge of the subtropical gyre in the Indian Ocean. Therefore, the zonal pattern in *G. inflata's* distribution is centered on a consistent flow to the east throughout these basins. This brings forth a question: How does this species maintain itself in a unidirectional zonal flow? There must be some mechanism to recruit individuals to the upstream area off South America in order to maintain the population against advection.

It is apparent from the dynamic height field that this recruitment is not taking place to any major degree in the mean circulation around the gyre. The extension of high relative abundance in the Benguela Current off the east coast of southern Africa follows the mean flow but suggests this extension of the pattern is a net loss to the mean population, since the species disappears as one proceeds northward along the dynamic height contours. In contrast, the cosmopolitan and subtropical species shown in figure1(b,c) mirror the circulation in the gyre in terms of the areas where they make their maximum contribution. The highest percentage composition of both of these species are found in the restricted closed portions of the South Atlantic gyre along the South American coast.

A second correlation between the characteristics of the large-scale circulation and the biogeographic distribution of transition species is seen by comparison of figure 1(a) and figure 3(b). The zone of highest relative abundance in *G. inflata* corresponds closely to a band of high eddy energy across the poleward edge of the subtropical gyres. The eddy available potential energy is a measure of the intensity of the mesoscale (50 to 200km scale) eddy field.These components of the eddy field lead to temporal variations on a time scale of two weeks to several months. The zones of high eddy energy such as that across the basins in figure 3(b) are areas with high horizontal diffusion as well as vertical exchange. These eddy-induced effects in combination with lateral variations in other environmental parameters such as nutrients (Fig. 2), and some rather special processes occurring in nonlinear features of the eddy field discussed below, make the transition zone a unique environment.

COHERENT EDDIES, RECIRCULATION, AND FRONTS

As part of the eddy field there exist features which can persist for substantial periods of time. Rings are one case of this type of feature. These eddies have their own inherent capability to drift to the west. In the situation where the flow around the ring or eddy is larger than its translation they can carry fluid with them as they move. In some parts of transition zones then, the eddy field may play an important role in recruiting individuals upstream against the mean flow. This can occur in the case of Gulf Stream rings, for example (Ring Group, 1981); although, the evolution of the ring itself in time may limit the effectiveness of this process. Typically, the ring become effective transport mechanisms only for those few species which have the ability to exploit the ring environment (Wiebe & Flierl, 1983).

Western boundary current systems also have closed recirculations of quasi-stationary nature associated with them. The best described of these is the Gulf Stream recirculation in the western North Atlantic. This feature is nearly a quarter the size of the entire subtropical gyre and therefore has a fairly long recirculation time, approximately six months to a year. This system correlates with a relative abundance maximum in *G.glutinata* similar to the one observed off Brazil in figure 1(c). A pair of recirculation cells are reported off the coast of Brazil by Tsychiya (1985). The highest percentage of abundance for *G.glutinata* overlay the southern of these two recirculations.

The western extreme for the transition species, *Globorotalia inflata*, occurs in proximity to the region where the Brazil/Falklands (Malvinas) confluence loops offshore. The trajectories of satellite tracked ARGOS drifters deployed in the confluence and upstream in the Brazil Current from October/November 1984 to June 1985 are shown in figure 4. These pseudo-Lagrangian instruments provide a crude measure of the drift patterns expected in the plankton community. Over the nine months deployment period all but two of the drifters were swept through the confluence region and out into the eastward flow across the southern edge of the gyre. Many of the trajectories, however, show a region of prolonged residence time thus indicating a partially trapped region in the flow centered at approximately 39°S and 49°W. Drifters are retained in the 78,000km^2 area approximated by the circle in

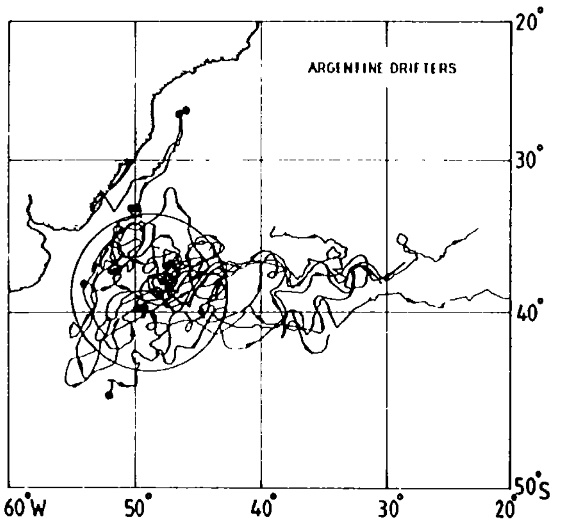

Fig. 4 Trajectories of nine ARGOS surface drifters deployed off South America from October/ November 1984 to June 1985. Circle denotes a region over which the residence time calculation discussed in the text was done. Dots indicate the launch points for the drifters.

figure 4 for an average of 3.8 months with two units remaining in the region over six months. This sort of maintenance in the region upstream of the broad flow extending across the gyre has sufficient residence time scales to provide contineous recruitment of individuals to the broad abundance maximum seen in species such as *G. inflata*. The effectiveness of recirculation regions such as the one off Argentina in maintaining a population against a steady loss due to mean advection depends on the reproduction rate of the organisms compared to their residence time in a region. As the generation time of the organism increases, a longer residence time in the recirculation is needed to sustain the population against the net advective loss.

A final physical phenomenon which is associated with transition zones is frontal activity. The focus of much of the discussion above has been the so-called subtropical front across the South Atlantic and southern Indian Oceans. This front is the core of the eastward transport and is responsible for the high eddy energy in this region. Fronts have important effects on ocean life from phytoplankton to large nekton. There is generally enhanced primary productivity in fronts for the reasons outlined above. Zooplankton and micronekton which maintain themselves in prescribed portions of the water column in the vertical, but restrict themselves to random motions in the horizontal, will be concentrated by the horizontal convergence tied to the existence of near surface fronts (Olson & Backus, 1985). Free swimming nekton may move themselves into fronts to make use of the higher concentrations of food. These positive aspects of the interaction between biological processes and the flow environment in fronts must be balanced against the problem of recruitment to the front in the face of net downstream advection, as discussed previously, and the stress induced by large change in physical and biological conditions tied to the environmental contrast across the front and the vigorous mixing in the frontal zone.

DISCUSSION AND CONCLUSIONS

Transition zones are areas where the nature of the large-scale ocean circulation and mesoscale features in the oceans' physical structure interact with biological factors to produce a unique environment. The contrasts in the environment between regions bounding transition zones and the vigorous eddy fields found in these regions lead to an admixture of fauna whose major distribution is either cosmopolitan, subpolar, or subtropical. Transition zones also have associated endemic forms which must overcome the net advective loss due to the unidirectional mean circulation in these zones in order to exist. This may be accomplished by a combination of reliance on the mesoscale eddy field or an ability in adults to withstand long periods in transit around the gyres. Tight recirculations close to the western boundaries may play an important role in recruitment of organisms into the upstream portions of the mean eastward flows. Fronts and an intensified mesoscale eddy field associated with transition zones are important in determining the distribution of animals and phytoplankton. The nature of fronts as boundaries between water masses and the enhancement of mixing along them leads to enhanced productivity and higher species diversity in their proximity.

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DISTRIBUTION OF MESOBENTHOPELAGIC FISHES IN SLOPE WATERS AND AROUND SUBMARINE RISES

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INTRODUCTION

Not unlike the vast majority of biogeographers who have tried to explain peculiarities in spatial distribution of the open-ocean pelagic organisms, I consider the present-day distributional ranges of the individual species as conditioned mainly by contemporary rather than historic causes. Recognition that correlations between the distributions of plankton (i.e. all organisms passively drifting horizontally together with their continuously moving medium) and water masses exist has been of utmost importance in open ocean biogeography. This approach applied for the first time by Haffner (1952) and elaborated by Brinton (1962), Ebeling (1962) and many other authors, has served as a base of the well-known theory (the so-called "water mass hypothesis") concerning the association of the distributional limits of planktonic organisms with water mass boundaries.

DISCUSSION

Among my compatriots, the late Prof. C. W. Beklemishev (1928-1983) made the most valuable contribution to this particular field: he elaborated in detail the concept of functional structure of distributional ranges for planktonic organisms in a moving environment, recognizing a "reproductive base(s) of the range" of the species, located within a more or less closed horizontal circulation(s), and both non-sterile and sterile expatriation areas resulting from expatriating currents (Beklemishev, 1969). The extent of those expatriation areas is determined by differing limiting factors including temperature, dissolved oxygen, biological productivity, etc. The variable tolerance to these factors among species having the same base(s) of range may result in the great diversity of their overall distributions in the ocean.

This approach allows us to recognize species groups with similar bases of ranges (which can be called "geographic elements of the fauna and flora"; ecologically, they are "recurrent groups") and use them for the biogeographic division of the ocean. The majority of ranges of relatively abundant mesopelagic planktonic fishes (as well as invertebrates), may be reduced to comparatively few main distribution types (Beklemishev et al., 1977; Parin, 1984). At the same time it should be mentioned that the ranges of some species do not fit such schemes (Parin & Bekker, 1981) and it is possible that the bases of their ranges are localized within the vertical circulation, as has been suggested by Bruun (1958).

The foregoing discussion relates only to open-ocean pelagic plankton species (including macroplanktonic fishes), distributed in the midwater environment and without any connection with the bottom and continental shores. It is known, however, that some species of what are essentially mesopelagic fish genera (also belonging to the macroplankton, or micronekton), live in slope waters and around submarine rises and by their habit, may be defined as bentho-pelagic forms in a broad sense (Parin & Golovan, 1976). These include permanent near-bottom dwellers, as well as species that migrate vertically to far above the bottom at night. The following examples may be tentatively given: *Triplophos hemingi* (Gonostomatidae), *Polymetme* spp., *Yarrella blackford.* (Photichthyidae), *Thorophos* spp., *Maurolicus muelleri*, *Argyripnus* spp., *Polyipnus* spp., (Sternoptychidae), *Odontostomias* spp. (Melanostomiatidae), *Idiolychnus urolampus*, *Diaphus adenomus*, *D. watasei*, *D. suborbitalis*, *Lampanyctodes* *hectoris* (Myctophidae), *Melamphaes acanthomus, M. suborbitalis* (Melamphaeidae), *Paroneirodes glomerulosus* (Diceratiidae), etc. (see also Merrett, 1986). A similar mode of existance is typical also for some nektonic fishes which are not considered in this report.

All the aforementioned benthopelagic macroplanktonic fish species are members of the "open-ocean" families widely distributed in the mesopelagic habitat: related species dominating in these families are characteristic for the open ocean. It seems impossible to explain the distribution of bentho-pelagic fishes from the point of view of the water mass hypothesis. In fact, the suggestion of a connection between the reproductive bases of their ranges and the stationary and quasi-stationary near-shore and island circulations does not fit with the almost complete absence of any considerable expatriation of such species into the adjacent open ocean (as should be observed according to the abovementioned concepts). Like their oceanic relatives all these fishes have pelagic eggs and larvae. Nevertheless, even the dispersion of early developmental stages appears to be very limited since they have been recorded in the open ocean extremely rarely. The eggs of *Maurolicus muelleri,* which are widely distributed in some areas of the Northern Atlantic (Serebryakov et al., 1983), are thought to be the most important exception. On the other hand, the early stages of slope dwelling myctophids and stomiatoids are very rare in the open sea. Therefore a more appropriate theory should be looked for to explain the existing distribution of bentho-pelagic fishes.

In my research I have drawn my attention to isolated maintaining populations of bentho-pelagic fishes dwelling on separate seamounts. The rather large population of a myctophid, *Diaphus suborbitalis,* inhabiting the Equator Seamount in the western tropical Indian Ocean (0°26'N, 56°01'E) can be regarded as one of the most striking examples of this kind (Parin & Prutko, 1985).

As with the majority of other Myctophidae this species shows diel vertical migration (Go, 1980). During these migrations, as confirmed by echograms, the Equator population rises to a 50-100m distance above the seamount at night and descends nearly to the slope over dawn (Fig. 1). Despite passing through strong (to 2.5 knots) and contrarily-directed currents during vertical migration, these fishes apparently always remain aggregated over the seamount, none having being caught at a distance of 2-3 miles from it.

I consider this as unequivocal evidence of the existence of navigatory orientation behaviour, the mechanism of which remains to be understood; it is evident, however, that the visual reception of the bottom is excluded. Therefore it is speculated that schools of *D. suborbitalis* are able to determine rather exactly their position in midwater relative to the site of their daytime residence and can actively counteract transportation out of the normal species habitat. Other bentho-pelagic macroplanktonic species that undergo diel vertical migrations seem to stay over the slope and near submarine rises in a

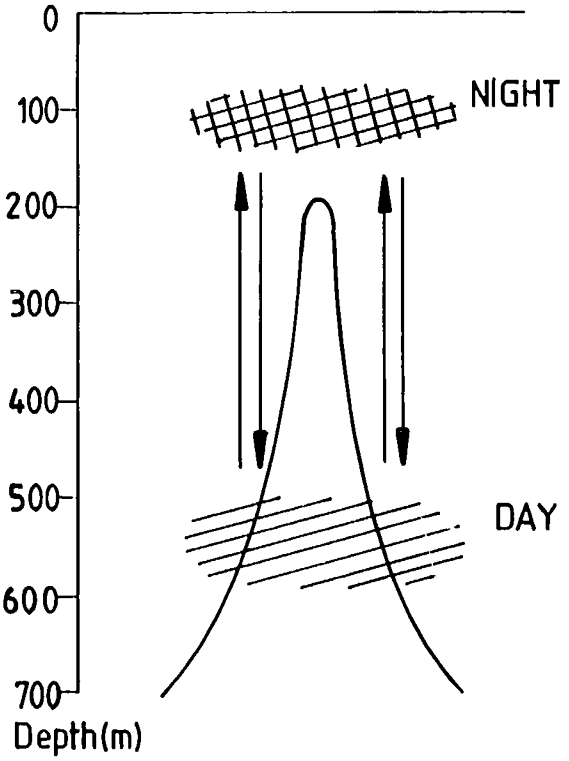

Fig. 1 A scheme showing diel vertical migrations of the myctophid fish, *Diaphus suborbitalis* over the Equator Seamount in the western Indicn Ocean.

similar way. Study of the imitation model elaborated by Rudyakov & Tseitlin (1985) of an independent fish population dwelling above a seamount has shown that such a population is able to be maintained and reproduce even when early developmental stages are dispersed by turbulent diffusion. In this case large numbers of larvae should be found downstream of the mount. This is not the case for the Equator larval population of *D. suborbitalis*. Development of these mesoplanktonic ontogenetic stages appears to proceed directly over the slope and rises but how they are contained within the nearshore environment remains unclear. However, local gyres (horizontal and/or vertical) of any spatial scale may exist - ones not stationary, but ones possessing a temporary stability commensurate with the duration of development time from egg stage to the actively orientated juvenile stage.

CONCLUSION

Therefore, one can conclude that two principal differences exist between closely-related, ecologically and behaviourly similar pseudoceanic bentho-pelagic and oceanic pelagic macroplanktonic fishes. The first difference consists of an absence of considerable dispersion of mesoplanktonic developmental stages for pseudoceanic forms: the previously suggested hypothesis which tries to explain this difference by rapid development of early stages in local gyres is not based on reliable facts but some parallels can be drawn with the situation in upwelling systems (Peterson et al., 1979). As far as the second difference is concerned (the absence of expatriation of adults of bentho-pelagic species into the open sea), my explanation of this phenomenon by the active selfholding in the habitat appears to be more well-founded.

Moreover, this explanation allows the conjecture that some oceanic pelagic species as well, are not always object to simple passive drift in water circulations, but rather can actively maintain their position within a certain part of the habitat. I realize that this conclusion contradicting my earlier views is paradoxical, but it is nonetheless quite applicable, if only to macroplankton (strictly, only to micronekton), and not to mesoplankton.

Finally, I wish to draw attention to the great similarity between the geographic ranges of bentho-pelagic macroplanktonic fishes dwelling above the slopes and rises and those of nektonic fishes inhabiting the same habitats. On the whole, the general types of distribution patterns typical for such fishes as mentioned above have nothing to do with the types of patterns typical for open-ocean species. However, the pattern for both groups of benthopelagic fishes fit quite well the division of the world ocean patterned according to the distribution of the shelf and neritic fauna.

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TROPHIC FACTORS AFFECTING THE DISTRIBUTION OF SIPHONOPHORES IN THE NORTH ATLANTIC OCEAN

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INTRODUCTION

In spite of the general lack of consideration given to siphonophores and the significant role that they play in marine ecosystems, there is a reasonable amount of information on their geographical distribution in the World's oceans, particularly for the North Atlantic. Much of the earlier data has been summarized by Margulis (e.g. 1972), who drew up distributional maps of 'total ranges', and broadly divided the species into boreal, tropical and equatorial forms. The patterns of distribution were considered to be consistent with those established for other planktonic/nektonic organisms and were related to the basic division of the oceans into various water masses. However, these 'total range' maps give no information on regional differences in the relative abundance of an individual species, nor do they take into account vertical distribution patterns (see Pugh, 1977). The latter situation partially was rectified by Margulis (1984), but again the conclusion were based on first and last capture principles.

Fasham & Angel (1975), using data on ostracods, demonstrated that it was necessary to consider all aspects of the regional, vertical and numerical distribution of the various species in order to establish faunal zones. They found that such zones, several of which could be present in any water column, were typified by the presence of certain species that had characteristic relative numerical abundances, and that it was rare for an individual species to be wholly confined to one zone. Many of these zones could be associated with hydrographical features, but for others the correspondence was not so apparent. A similar conclusion was reached by Pugh (1977) for siphonophores, and Fasham & Foxton (1979) for decapods. The general conclusion from all such studies, as succinctly summarized by Haedrich & Judkins (1979), was that the faunal change was not always abrupt, even in the region of major physical boundaries (see Domanski, this volume), and that there is not necessarily an absolute response by an individual species to a change in water mass. Other more subtle reasons may be affecting the distribution of pelagic organisms. This possibility is examined in relation to the distribution of siphonophores in the N.E. Atlantic, using data from ten stations located between the equator and 60^{0}N.

DISTRIBUTION PATTERNS

Certain underlying trends appear from these data, for example:-

1. Species diversity is highest in the warmer, more southerly waters around 18^{0}N (Fig. 1) and declines both towards the equator, and more markedly towards the north. This is a general feature for many groups of pelagic organisms.
2. Neither the numerical abundance nor the biomass (displacement volume) of siphonophores follows the same trend. The data for the 21 most abundant calycophoran species (nectophores only), show two peaks of numerical abundance, one between 11°N and 18°N, and the other between 40° and 50°N (Fig. 1). However, biomass tends to increase with increasing latitude and, overall, gelatinous organisms are very important contributors to the total biomass of pelagic organisms at higher latitudes.
3. The great reduction in the number of species towards the north is largely accounted for by the disappearance of near-surface living forms. These species, which can occur in large numbers in warm surface waters, mainly belong to the calycophoran families Diphyidae and Abylidae, and *Diphyes bojani* is taken as an example (Fig. 2A). In contrast, the increase in siphonophore

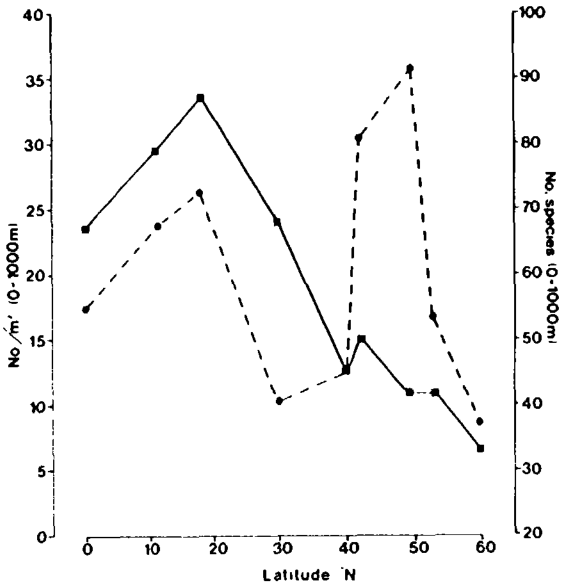

Fig. 1 The geographical distribution in the N.E. Atlantic Ocean (see Fig. 3 for exact positions) of the total number of siphonophore species (□—□) and the number of specimens m^{-2} (21 commonest calycophoran species) (O--O) present in the net samples collected in the top 1000m of the water column.

numbers between 40° and 50°N is caused by large numbers of a few deep-living species (e.g. *Rosacea* spp.)(Fig. 2 B,C) that mainly belong to the calycophoran families Prayidae, Hippopodiidae and Clausophyidae. These deep-living species, although commoner at higher latitudes, generally have widespread distributions.

The change-over between the geographical distribution and numerical abundance of the major calycophoran families of siphonophores can be related directly to the regional differences in biomass. The near-surface living abylids and diphyids are mainly small, active predators; the deeper living families are generally larger and slow moving. Although these major differences in the faunal assemblage of siphonophores in warmer and colder waters can be associated with various water masses (Pugh, 1977), there may be other factors that play more important roles. One such factor could be the dietary preferences of the individual siphonophore species.

Siphonophores are carnivorous animals, mainly feeding on crustaceans especially copepods, and undoubtedly they play an important role in the pelagic ecosystem. Recent studies by Purcell (e.g. 1980; 1981) have shown that siphonophores are selective feeders and the preferred diet of an individual species can, in general, be related to certain morphological and behavioural characteristics. Morphologically, there appears to be a direct relation between the size of the feeding polyps (gastrozooids) and the size of the prey captured. Behaviourally, although probably as a consequence of the morphology, those species with smaller gastrozooids tend to be more active and rapid swimmers*. There are also differences in feeding strategy (Biggs, 1977). Active swimmers frequently alternated between periods of swimming and 'fishing', and set, often complex, tentacular nets to ensnare their prey. Weaker swimmers tend to spend longer periods 'fishing', with their tentacles simply hanging down from the stem. These behavioural differences may be related to the fact that the swimming speed and activity of crustacean zooplankton generally increases with size (Mauchline, 1972). Thus, the larger siphonophores simply have adopted a 'sit in wait' strategy since the chances of encountering a suitable, large prey item are increased by the latter's greater activity. Similarly, the lesser abundance of such prey can be offset against the energy savings resulting from the siphonophore's lack of swimming activity.

The question thus arises as to whether these differences in dietary preference and behaviour, for the two sharply distinct siphonophore assemblages in the warmer and colder waters of the N.E. Atlantic, can be correlated with geographical and vertical differences in the distribution of their preferred prey? Although, unfortunately, a fully comparable data set for potential prey items e.g. copepods and ostracods, is not yet available, there appears to be some general evidence to support this supposition. Within a single water column there is a general trend for the mean body size both of an individual species (Bergmann's rule-see Mauchline, 1972)

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*the discussion here is limited to the calycophoran species, as these are the only ones sampled quantitatively by nets - see Pugh (1984).

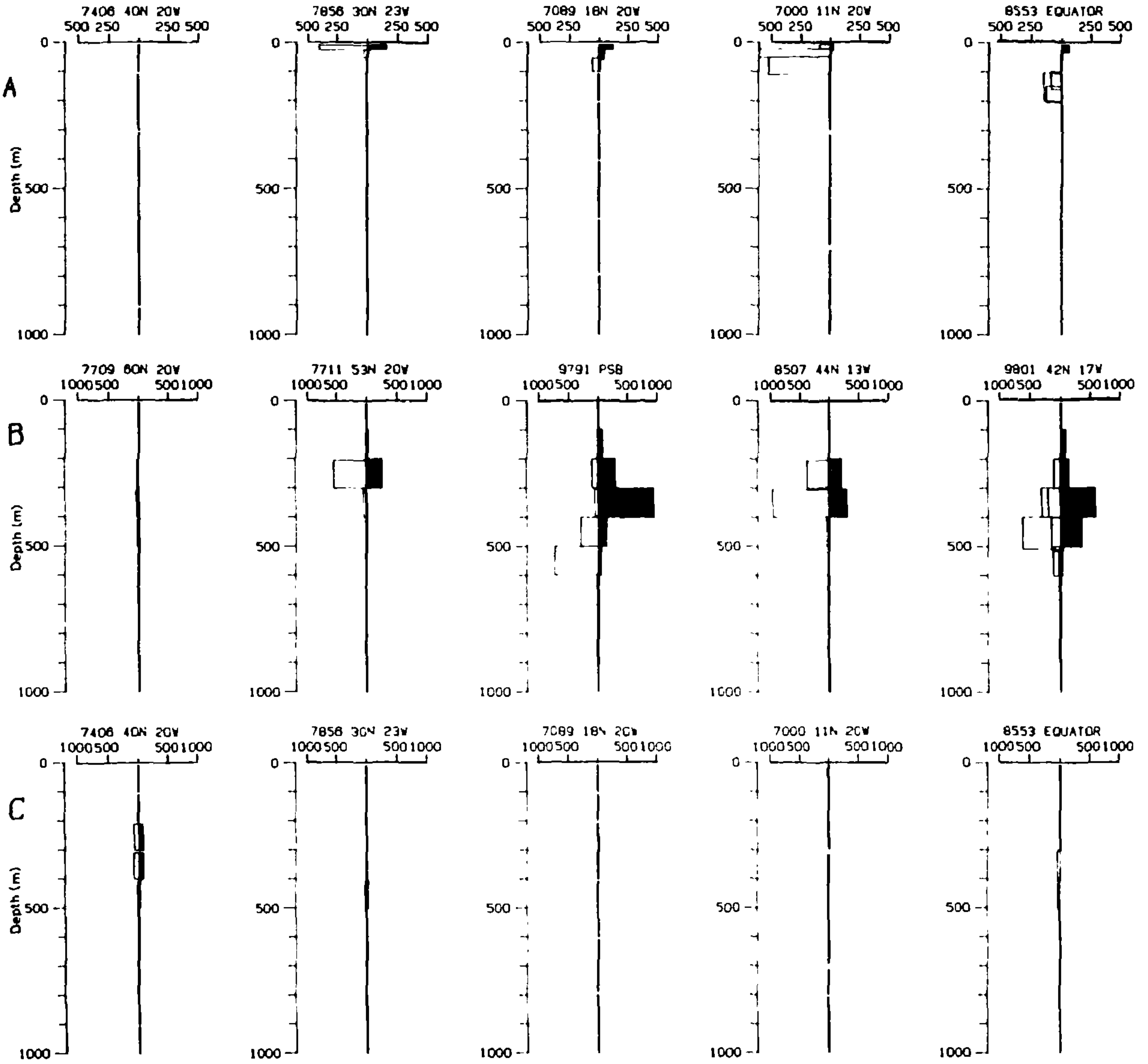

Fig. 2 **A** The vertical distribution of *Diphyes bojani*, by day and night (left and right of ordinate, respectively). Number of anterior nectophores/$10^4 m^3$, at various localities (see headers) in the warmer waters of the N.E. Atlantic Ocean. No specimens of *D. bojani* were found north of 40°N. **B** - **C** The vertical distribution of *Rosacea* spp. at various localities in the N.E. Atlantic Ocean. Number of nectophores/$10^4 m^3$. PSB= Porcupine Seabight ca. 49°30'N, 14°W; Equator= 0°N, 22°W. The numbers in the headers for each histogram refer to RRS 'Discovery' Station numbers, except for Sta.7000 which is an amalgam of 'Discovery' Sts 6662 and 7824.

and of a taxonomic group, particularly crustaceans, to vary inversely with temperature, at least within the top 700-1000m of that water column. Thus, Roe (1972) found, for copepods in the top 1000m of the water column around the Canary Islands, that 57% of the total displacement volume occurred within the 500-600m depth range, while ca. 30% of the total numbers were present at the shallowest depths (40 and 50m) sampled. The vertical distribution patterns of siphonophores (Pugh, 1974), and their projected dietary preferences, fit in well with this general scheme of increasing prey size with depth. The preponderance of small items, e.g. copepods and ostracods (see Angel, 1979) in near-surface warm waters can be linked with the presence there of small actively swimming siphonophores, many of which undergo diel vertical migrations (Pugh, 1977). At deeper depths the larger mean body size, but lesser abundance, of the prey would suit the presence of larger, less active siphonophore species, and these do predominate there.

In order to explain the disappearance of small, shallow-living siphonophore species at more northerly latitudes on the same basis it would be necessary to find a concomitant decrease in small prey items. Certainly, as with depth, there is a trend for an increase in the mean body size of a population in the colder, northerly waters (e.g. Grice & Hulsemann, 1965), but in the superficial layers of such waters the situation is complicated by the moderately large seasonal changes in temperature. Thus Deevey (1960) found that, for certain copepod species, not only was there an inverse relation between body size and water temperature, but also a direct correlation between mean size and the quantity of phytoplankton material available. This might be related to the large seasonal fluctuations in primary productivity, but it is probable that a more important factor is the seasonal change in the size distribution and specific composition of the phytoplankton population itself (Holligan & Harbour, 1977). The body size of the herbivore thus being directly related to the mean size of the available phytoplankton cells. If this relation also holds between the siphonophores and their potential prey, then one might expect seasonal fluctuations in the specific siphonophore population, and its numerical abundance, but unfortunately insufficient data are available in this context. However, the northward spreading of certain shallow-living siphonophore species during the summer months (unpubl. data) would be consistent with this.

Other data also indicate a marked geographical change in the size distribution and abundance of potential prey. For instance, the ostracod population in the top 300m of the water column at 30°N 23°W and at 44°N 13°W (Angel 1977; 1979) were markedly different, with large numbers of small species being present at the former position, whereas overall numbers were very low at the latter. Below 300m depth, the population numbers at both stations were very similar. These facts can be related to the distribution of hippopodiid siphonophores, for Purcell (1981) found that the near-surface living species, *Hippopodius hippopus,* fed almost exclusively on ostracods. Thus, it was not surprising to find that *H. hippopus* was common at 30°N, but was totally absent at the 44°N site. If one can extrapolate these dietary requirements to the closely related species, of the genus *Vogtia,* then the deeper depth distribution of these means that they could exploite the larger-sized ostracod population present at all latitudes.

However, with regard to the potentially more important prey, copepods, Roe (1984) found that, at 44°N 13°W, small *Clausocalanus* spp. predominated at four depths, between 100 and 600m, whereas in the Canary Island region these species were concentrated at the shallowest depths and were less abundant (Roe, 1972). Nevertheless, the total number of copepods was far greater at 44°N than further south, the enhancement in numbers being particularly marked at the deeper depths sampled, and this could be associated with the increased number of deeper-living siphonophores found at more northerly latitudes.

CONCLUSION

Thus, despite the necessarily superficial nature of the comparisons, it is concluded that the size distribution and abundance of the potential prey population at any one locality and depth plays an important role in determining the structure of the specific siphonophore assemblage associated with it. As Headrich & Judkins (1979) concluded, it is relatively easy to establish correlations between variations in the hydrological conditions and the distributions, both vertically and horizontally, of certain species, but other underlying factors, such as trophic relations, may be playing a more immediate part in controlling these distributions.

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ZOOGEOGRAPHY OF THE INDIAN OCEAN ZOOPLANKTON : CONCEPTS AND CONSTRAINTS

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INTRODUCTION

The Indian Ocean is cut off in the north by the Asiatic land mass. This coupled with the monsoonal reversal of surface gyres (see Nair, this volume) results in the distribution of physical and chemical properties typifying the northern Indian Ocean. Known zooplankton distribution patterns and possible zoogeographic zonation were reviewed by Rao (1979) and in the atlas of Van der Spoel & Heyman (1983). In the present contribution knowledge of pattern in the distribution of Indian Ocean zooplankton is briefly reviewed on a within and between ocean basis.

WITHIN OCEAN PATTERNS

There exists little evidence of biogeographic difference between the Bay of Bengal and the Arabian sea. This is despite the fact of known differences in physical and chemical parameters (Sengupta & Naqvi, 1984; Wyrtki, 1973) and in the strength of the SW monsoon, which is stronger in the Arabian Sea, (see Nair, this volume). Despite delimitation of the eastern/western distributional limits of the copepods *Labidocera pectina* and *L.rotunda* (Fleminger et al., 1982) in the Andaman Sea and the apparent absence of the cephalopod *Onychia carribea* in the Arabian Sea (Van der Spoel & Heyman, 1983), present knowledge indicates that the epipelagic region of the entire northern Indian Ocean is a single biogeographic unit.

Despite evidence that the hydrochemical front at 10°S (Wyrtki, 1973) acts as a barrier in the case of certain pteropod (Sakthivel, 1973) and euphausiid species (Brinton & Gopalakhrishnan, 1973), this is not the case for oceanic chaetognath or ostracod species (Nair & Madhupratap, 1984), which show southern distributional limits between 28°S and 42°S. There appears to be a decrease in abundance south of 10°S for species that occur on either side of the supposed boundary, presumably related to the demarcation by the front of nutrient-enrichened waters of the monsoonal gyre from nutrient - depleted waters of the subtropical gyre (Vinagradov & Voronina, 1961; Timonin, 1971; Lawson, 1977).

BETWEEN OCEAN PATTERNS

Differences in species composition between oceans (tropical and subtropical) may depend in part on depth of occurrence. Thus for calanoid copepods there appears to be much higher overlap between the Atlantic and Indian Oceans for deep-living species (92% overlap between North Atlantic and Arabian Sea, Grice & Hulsemann, 1967) than for surface-living oceanic forms (60% overlap between Atlantic and Indian, 91% overlap between Indian and Pacific). Similar patterns are seen in epiplanktonic chaetognaths (Nair & Madhupratap, 1984). The differences may be related to the greater effectiveness of the barrier (Africa) between the Atlantic and Indian than that of the barrier (Australasian seaway) between the Indian and Pacific Oceans.

Although biomass equitability among calanoid copepod species is higher in the open ocean than in estuarine or neritic situations (Madhupratap, 1983), studies on epipelagic calanoid copepods (Madhupratap & Haridas, in the press) show the dominance of relatively few species in the open ocean. Dominance is sometimes considered an index of ability to disperse effectively (Briggs, 1974). Of the 22 dominant (those consistently >1% of the total copepod fraction) epipelagic copepod species occurring in the northern Indian

Ocean, 13 have circumglobal distributions and all the rest are Indo-Pacific.

CONCLUSIONS

It is obvious from these studies that knowledge of distribution patterns is limited to species within a quite restricted sort of groups, among them Copepoda, Chaetognatha, Pteropoda and Euphausiacea. Even within these groups knowledge for most species is typically sketchy, with few studies approaching the completeness of that on *Pontellina* by Fleminger & Hulsemann (1974). Much more basic, synoptic systematic work is prerequisite to discussion of current and past distribution patterns of zooplankton of the Indian Ocean.

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VICARIANCE ICHTHYOGEOGRAPHY OF THE ATLANTIC OCEAN PELAGIAL

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INTRODUCTION

The history of the formation of the Atlantic Ocean makes it possible to reconstruct the origin of different vicarious forms of pelagic ichthyofauna. There have been several stages in the formation of the Atlantic Ocean which determined composition, taxonomic interrelations and geographical distribution of the ichthyofauna of this water body. The separation of the American and African continents initiated this formation process. An equally important phenomenon was the presence for a long period, including the Cretaceous, of the Tethys Sea. Settlement in the Atlantic Ocean of tropical and warm-temperate groups of epipelagic fish of Indo-West Pacific origin was possible via the Tethys, though extinction of these elements followed in the Tertiary (Berg, 1955; Briggs, 1974). The development of the ichthyofauna was strongly influenced by the emergence of the Central American Isthmus separating the Atlantic from the Pacific waters and establishing the present North and Equatorial Atlantic circulations (Herman, 1979). A more recent event was the glacial age with alternating cooler and warmer periods, terminating in a recent warming up of North Atlantic Arctic waters. Two other vicariant events are of significance:

1. the emergence of the Peninsula of Florida (Miocene) separating the previously continuous "Carolinian" fauna,
2. the drying-up (3-4 million years ago) and subsequent refilling of the Mediterranean leading to a relatively recent, impoverished and partly endemic Mediterranean fauna.

The epipelagic fish fauna of the Atlantic Ocean proper is likely to have been formed during the later half of the Tertiary, mainly in Oligocene and Miocene times. Unlike the West Pacific ichthyofauna it contains no Paleocene or Upper Cretaceous relicts. The ichthyofaunas of the tropical-equatorial regions on both sides of the oceans are somewhat different (Rass, 1980).

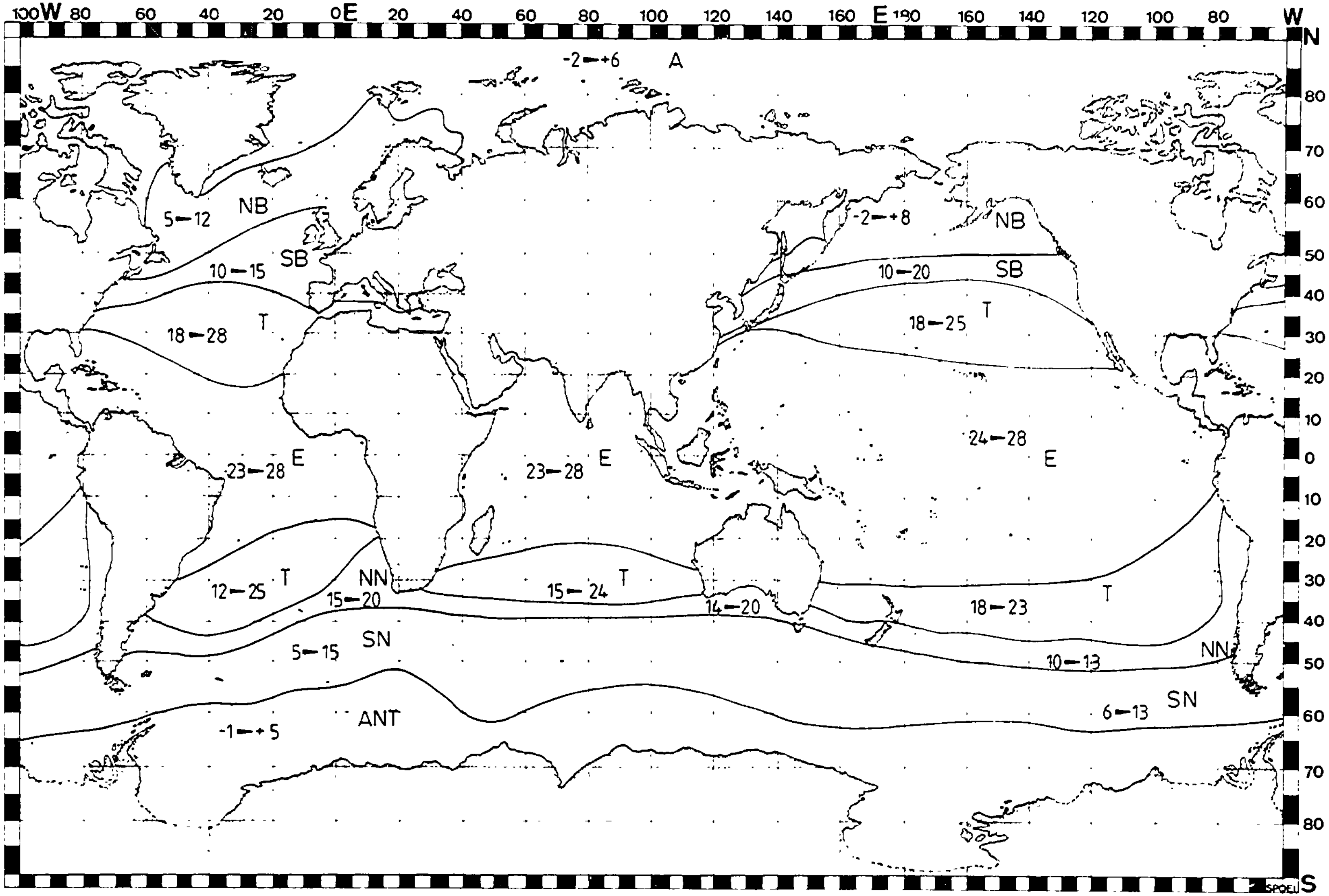
The pelagial of the Atlantic Ocean encompasses a greater diversity of climatic zones as compared to other oceans (Schott, 1942), and it was formed later than that of the Pacific and Indian Oceans. Especially the epipelagic ichthyofauna, which strongly reflects the pattern of climate belts, is different from that of other basins (Fig. 1).

VICARIANCE

The ichthyofauna of the Atlantic Ocean contains both purely coldwater cryopelagic genera and species in the Arctic and Antarctic, and purely equatorial-tropical genera and species isolated by the ichthyofauna of temperate waters. However, the genera and species which occupy similar ecological niches in the different regions of the Ocean can be considered to replace one another, representing vicarious groups differing taxonomically.

Vicariance, when used in connection with the geological past, e.g. in relation with the Panama Isthmus, is the phylogenetic concept (sensu Nelson & Platnick, 1981, but here it is used in the original meaning (sensu Mayr, 1963) and taken to mean an ecological and topological replacement. Zoogeographic studies would be more clear if terms and concepts be used in their original meanings. The boundaries of (ecologically) vicarious, not necessarily taxonomically related, forms from adjacent climatic regions generally overlap and competitive relations are observed with alternating predominance of one or another vicarious species depending on climatic gradients and other factors such as, for instance, selective fishing.

The recognition of (ecologically) vicarious species in the pelagial is, therefore, of consider-



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SPOELL

able interest from a theoretical as well as a commercial point of view (Rass & Carré, 1980).

Topologically distinguishable are the epipelagic and the mesopelagic, the nerito-pelagic and the oceanic-pelagic ichthyofaunas each containing both planktophagous and ichthyophagous species (Parin, 1968). The basis of ecological vicariance is the similarity of ecological niches mainly determined by food habits. The delimitation of the ranges of vicarious species is due to differences in temperatures at which reproduction is still possible. Temperature limits the reproductive range more than the overall range, since fish are usually more stenobiontic during reproduction than during other periods of their life. Distribution related to environmental temperatures usually parallel latitudinal climatic regions. Typical spawning temperatures vary between -2 and +5-6°C for coldwater Arctic and Antarctic species, mainly between +3 and 9-11°C for cold-temperate northern boreal and southern notal (cold-temperate waters of the southern hemisphere, SN in Fig. 1) species, between 8-10 and 15-20°C for tropical and between 21 and 29°C for equatorial species (Rass, 1977).

VICARIANCE IN OCEANIC TAXA

Meridional vicariance, always of the ecological type, can be observed in both oceanic pelagic and neritic pelagic species, while amphi-Atlantic vicariance, which may also be of a phylogenetic nature, is traceable only in neritic pelagic species separated by open ocean waters. Epipelagic planktophagous fishes are particularly oceanic and frequently show meridional vicariance. For example, the polar cod (*Boreogadus saida*), the Arctoboreal capelin (*Mallotus villosus*), the northern boreal Atlantic herring (*Clupea harengus harengus*), together with the mesopelagic planktophagous redfish (*Sebastes marinus*), the saury (*Scomberesox saurus*), and together with the predominantly mesopelagic blue whiting (*Micromesistius poutassou*) form a series of ecological vicariants from north to south. Continuing in a southward direction, the flying fishes (*Exocoetus* spp., *Cypselurus* spp.) and the Antarctic sidestripe (*Pleurogramma antarcticum*) make the series complete. The last species is ecologically similar to the polar cod, but its distribution range has not yet been studied exhaustively.

The ranges of some of these planktophagous species are closely related to the ranges of particular pelagic ichthyophagous species. Examples are provided by the distribution range of the saithe (*Pollachius virens*) corresponding to that of the herring, by the distribution areas of mass species of tunas (*Thunnus* spp.) and dolphinfishes (*Coryphaena*) corresponding to those of flying fishes (Exocoetidae) in the tropical.

VICARIANCE IN NERITIC TAXA

The borders of vicarious oceanic pelagic species are sometimes similar to patterns of neritic pelagic planktophagous species in the temperate waters of the western and eastern coasts of the Atlantic boreal and notal zones and to patterns of the amphi-Atlantic vicarious genera such as bitemperate(antitropical) anchovies (*Engraulis* spp.) and horse mackerels (*Trachurus* spp.)

Bitemperate genera are represented in waters of the southern part of the boreal zone by the North American and European anchovies (*E. eurystole*, and *E. encrasicolus*) and horse mackerels (*T. lathami*, *T. trachurus*) which are replaced in the corresponding waters of the notal zone by South American and South African species (*E. anchoita*, *E. capensis* and *T. lathami australis*, *T. capensis*). These species are meridional ecological vicariants and amphi-Atlantic ecological as well as phylogenetic vicariants. An excellent example of the amphi-Atlantic phylogenetic vicariance is provided by anadromous shads (*Alosa* spp.) occurring in the southern part of the boreal

Fig. 1 Climatic-biogeographical regions in the World Ocean and range of their mean monthly temperatures. A - Arctic, NB - northern Boreal, SB - southern Boreal, T - tropical waters, E - equatorial region, NN - northern Notal, SN - southern Notal, ANT - Antarctic.

waters off western Europe from the Baltic Sea to northern Africa and in the basin of the Mediterranean Sea (five species) as well as off North America from the Gulf of St.Lawrence to Florida (six species.).

In the western coastal waters of the Atlantic Ocean the species *Brevoortia tyrannus, B.patronus, B.smithi, B.aurea* and *B. pectinata* of menhaden are meridional ecological vicariants. In the eastern coastal waters of the Atlantic Ocean meridional ecologically vicarious distributions are distinctly shown by several clupeoids: sprat (*Sprattus sprattus*) in the European boreal waters proper, pilchard (*Sardina pilchardus*) in the southern boreal zone, sardinella (*Sardinella aurita*) in the tropical-equatorial waters and South African pilchard (*Sardinops ocellata*) in the northern notal waters.

Of special interest are phylogenetic vicarious interrelations between the pelagic ichthyofauna of the Atlantic Ocean and the Pacific Ocean ichthyofauna (Ekman, 1953; Rosenblatt, 1967) In origin these species result from geographic isolation, but as we are dealing here with a geological phenomenon affecting a whole fauna and different taxonomic groups, it should be considered a vicariance event. Examples of amphi-American vicarious relations are found in clupeoids (*Opisthonema oglinum,* and *O.libertate, Harengula* spp. and *H. thrissina*), anchovetas (*Cetengraulis edentulus* and *C.mysticetus*) and carangids (*Chloroscombrus chrysurus* and *C. orqueta, Decapterus macarellus* and *D.scombrinus*)

CONCLUSIONS

The arctoboreal capelin is represented in the Atlantic and Pacific Oceans by different subspecies, probably separated by glaciation in Pleistocene time. The northern boreal Atlantic herring was represented in the Eocene by related species in Europe and must have generated the related White Sea - Pacific herring (*C.pallasi*) in the Miocene.

The bitemperate subspecies and species of sauries, anchovies and horse mackerels must have formed during the Oligocene cooling, diverging northward and southward of the equator during the subsequent warming-up of the Equatorial waters (Berg, 1933; Hubbs, 1952). For this phenomenon it is therefore not evident which kind of vicariance is concerned. The West Atlantic menhaden species and East Atlantic species of pilchard and sprat are also likely to have become separated in Oligocene and early Miocene time. The anadromous shads must have moved from east to west somewhat later, probably in early Pleistocene time. Not long before the uplift of the Central American Isthmus, probably in Pliocene time, the tropical amphi-American group of *Opisthonema, Harengula* and *Cetengraulis* came into being and supplemented the group of epipelagic species of *Decapterus* and, possibly, *Chloroscombrus,* which had come with Tethys waters. And, finally, the most recent settlers in the Atlantic Ocean waters, probably as recent as Holocene, are a group of several genera of Indo-West Pacific genesis - Exocoetidae, *Sardinella* and *Sardinops.*

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EPIPELAGIC MEROPLANKTON OF TROPICAL SEAS: ITS ROLE FOR THE BIOGEOGRAPHY OF SUBLITTORAL INVERTEBRATE SPECIES

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INTRODUCTION

Epipelagic meroplankters are the larvae of benthic invertebrates that have been carried offshore from the continental shelf or the coast of oceanic islands either by eddy diffusion or advective processes. Among the latter may be included such phenomena as "rings", as encountered in the Gulf Stream system of the western North Atlantic (Flierl & Wroblewski, 1985) and quasigeostrophic mesoscale eddies seen off the Hawaiian Islands (Lobel & Robinson, 1983; in the press) that affect dispersal both toward and away from coastlines. The existence of invertebrate larvae of benthic species far out in the open ocean has been known since the Plankton Expedition, the results of which were reported in a series of volumes published near the end of the last century (polychaetes and sipunculans: Hacker, 1898; gastropod and bivalve molluscs: Simroth, 1895; echinoderms: Mortensen, 1898). The possible significance of these early observations apparently was not considered by biologists at that time, and it was not until the last two decades that systematic investigation of the epipelagic meroplankton was undertaken (Mileikovsky, 1966; Robertson, 1964; Scheltema, 1964; 1966; 1968; 1971a; b). These studies were largely restricted to the North and South Atlantic Oceans, from which a variety of invertebrate larval types have been described. Most larvae studied from epipelagic waters retain their competence to settle (Scheltema, in the press), and it is inferred from such observations that teleplanic larvae can delay settlement over long periods of time until they encounter an adequate cue for settlement.

Teleplanic larvae often show special adaptations for a long planktonic life. Among gastropods many species have long periostracal spines and very light, sometimes completely uncalcified, shells (Pechenik et al., 1984; Richter, 1984). Cymatiidae have particularly long velar lobes used for swimming as well as feeding (Fig. 1), and there is some indirect evidence in older veliger larvae for metabolic changes related to their long planktonic existence. Other invertebrate groups with teleplanic larvae also show some morphological modifications seemingly related to a long larval life.

In this account I propose to summarize the present knowledge about the occurrence of meroplankton throughout the tropical waters of the world and to discuss briefly the possible overall significance of long-distance dispersal. Only the larvae of prosobranch gastropod molluscs will be considered here as an example, since they constitute one of the most frequently occurring taxa with teleplanic larvae (Scheltema, in the press, Table I).

METHODS

Data on the occurrence of teleplanic gastropod-veliger larvae were collected in the tropical Atlantic Ocean over the past twenty years mostly on ships of the Woods Hole Oceanographic Institution, incuding R/V ATLANTIS II, R/V CHAIN, R/V KNORR and R/V CRAWFORD and include 412 locations. The Pacific Ocean samples were obtained by expeditions of the Scripps Institution of Oceanography over the past 26 years and were augmented by a cruise of the R/V ATLANTIS II in 1979 between Wellington, New Zealand and Honololu, Hawaii. A total of 337 locations are represented. Samples from the tropical Indian Ocean are from the Lusiad Expedition I and II taken during 1962 by the R/V ARGO of the Scripps Institution of Oceanography

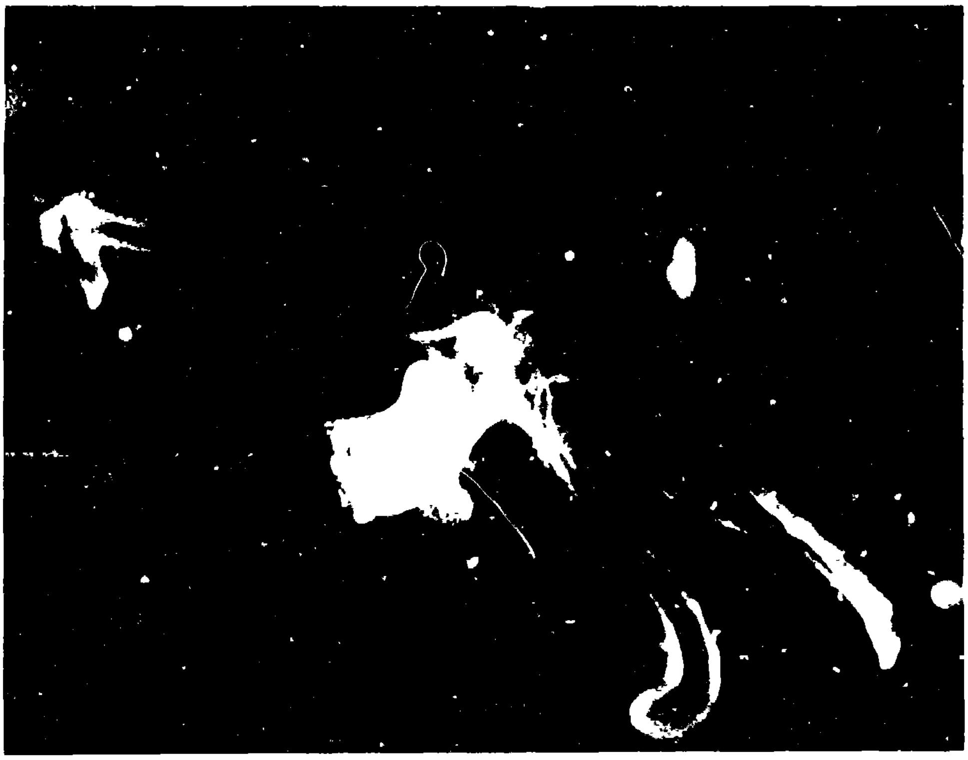


Fig. 1 Teleplanic veliger larva of a cymatiid, referred to *Cymatium labiosum* (Wood 1928) from the Gulf Stream in the western North Atlantic Ocean. The larval shell may exceed 5mm in length and is dark amber. There is an elaborate pattern of short, soft, periostracal spines giving a hirsute appearance (see, Scheltema 1971b, Fig. 32 : 21). *Cymatium labiosum* is known in the western Atlantic from North Carolina to Brazil, the Caribbean, Bermuda and throughout the Indo-Pacific including Hawaii.

and included 48 stations. The samples were taken by oblique tows from the surface to depths of ca 150 to 200m and were made with nets of either 3/4 or one meter diameter with a mesh of 240 to 360µm (usually the former).

RESULTS

The distribution of veliger larvae of gastropods are figured on maps of the tropical Atlantic, Pacific and Indian Oceans (Figs 2, 3 and 4). Specifically designated are those locations where larvae belonging to the gastropod families Architectonicidae and Cymatiidae were found. In the initial sorting 18 families of gastropods were readily recognized and the rank order of their occurrence in the Pacific is summarized in Table I. This order of abundance is largely the same as that in the Atlantic and Indian Oceans, though samples from particular expeditions sometimes showed reversals of the most abundantly encountered families. At least 70% of all open ocean samples taken in tropical waters contain teleplanic gastropod larvae with the exception of the tropical region between 120° and 160°W in the East Pacific.

DISCUSSION

The question arises as to the significance of all these larvae so widely distributed in the epipelagic waters over such large regions of the world's tropical oceans. What role do these larvae play in the geographic range of the species? This

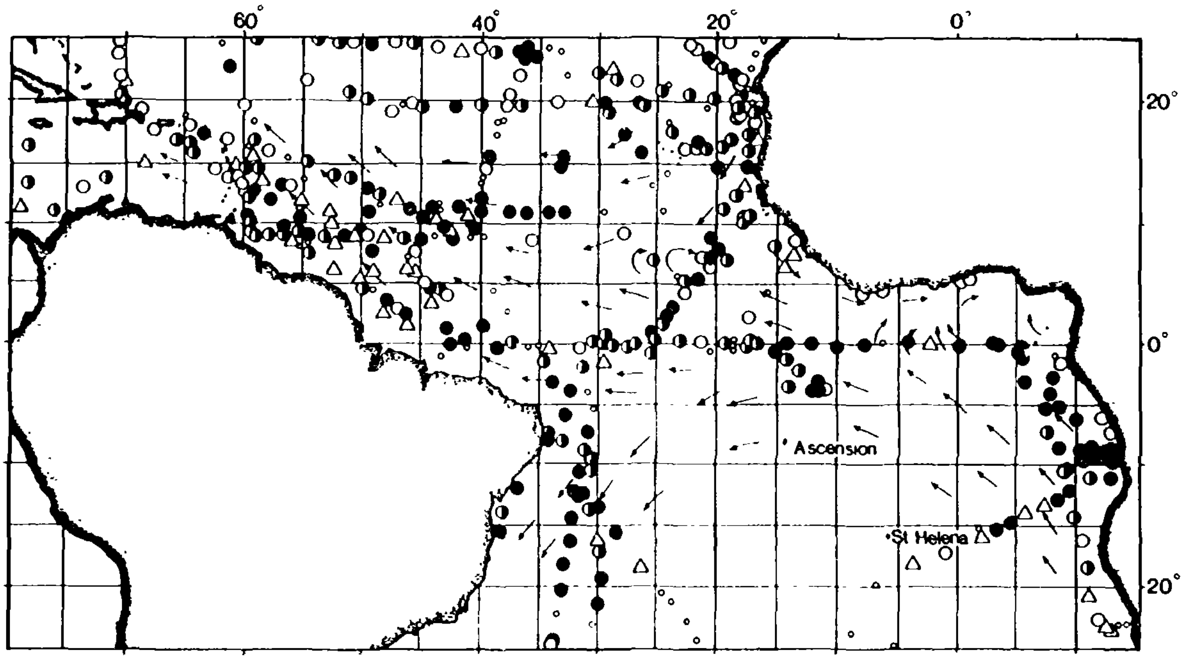
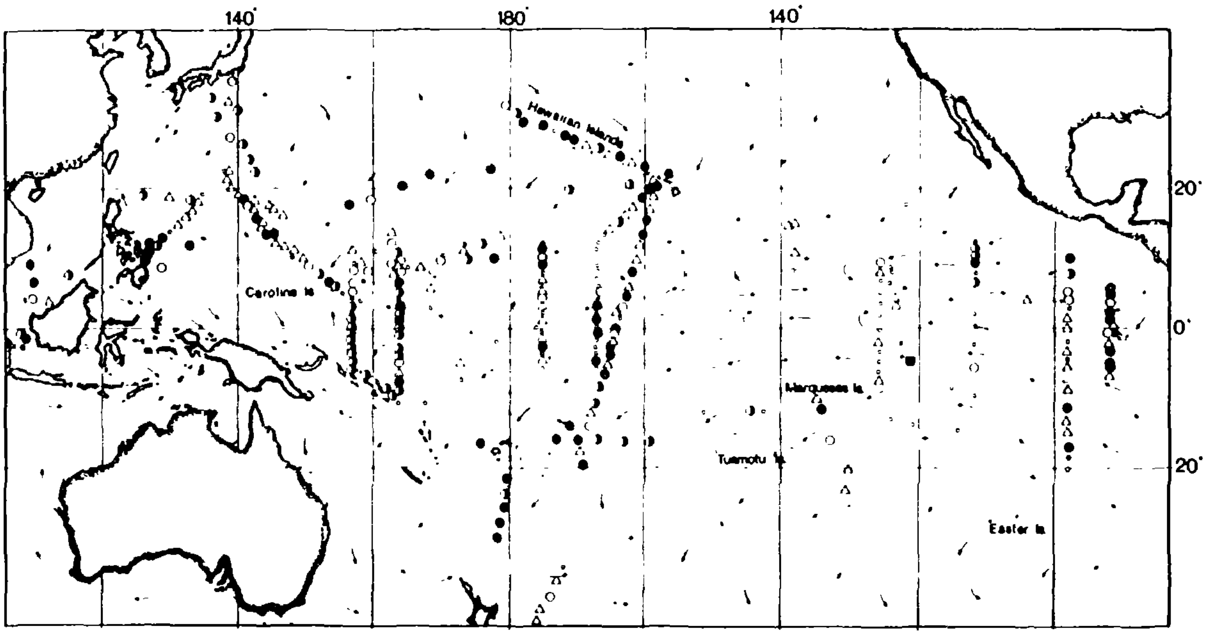


Fig. 2 Distribution of teleplanic gastropod veliger larvae in the epipelagic of the tropical Atlantic Ocean. Data are from 412 plankton tows. Large circles and triangles indicate localities where veligers were found. The small circles are positions where plankton tows were taken but no gastropod larvae appeared in the sample. Large, filled circles= Architectonicidae; large, open circles= Cymatiidae; divided circle (half-filled and half-open)= stations where both architectonicid and cymatiid veligers were found. Triangles show points where veligers of other coastal benthic gastropod species were found. Arrows indicate major surface circulation. (Distributional data modified from Scheltema, 1978; 1979 with some additional data added.)



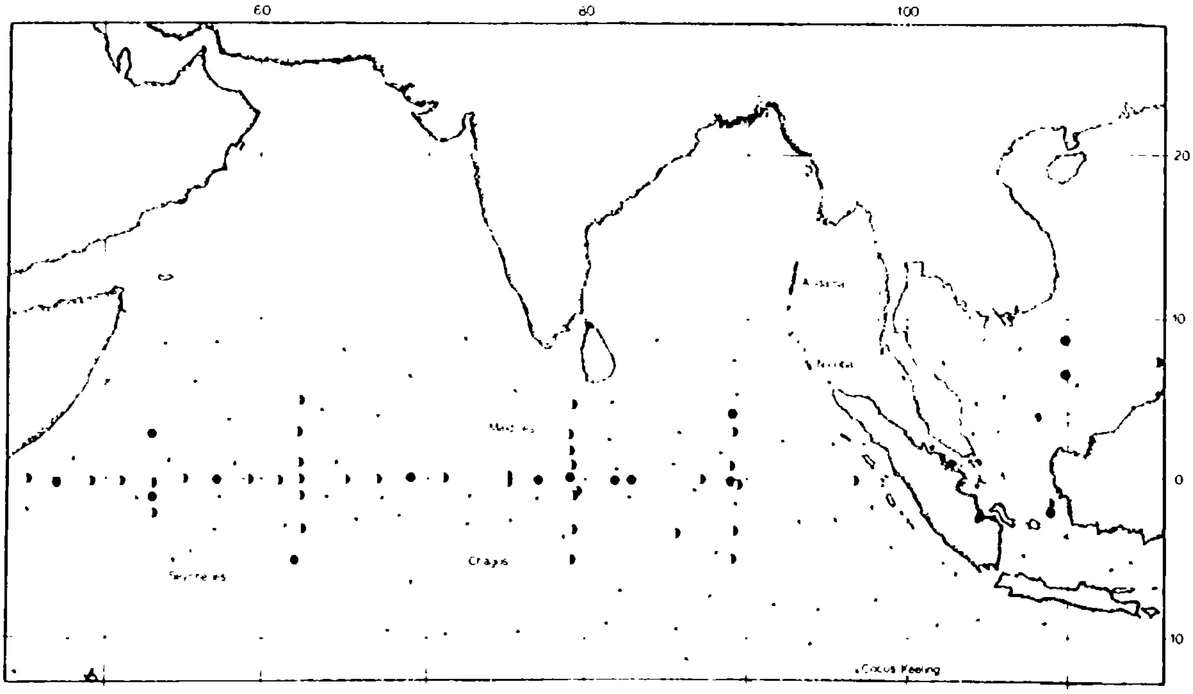


Fig. 4 Distribution of teleplanic gastropod veliger larvae in the epipelagic of the tropical Indian Ocean. Data from 48 plankton tows. All stations included gastropod veliger larvae. Surface current for the month of August shown by arrows were determined during the period when plankton was collected. (Currents generalized from Taft & Knauss, 1967: Fig. 5). Symbols as in figure 2.

question does not have a simple answer; it is necessary to understand not only how species are dispersed but also what constraints there are for dispersal, namely the ecological and biogeographic barriers that determine where species may survive and reproduce.

No matter where a teleplanic larva is carried by ocean currents, there are ecologic conditions, viz. physical and biological attributes of the environment, that will limit spatial distribution of a species both within and also at the limits of its geographic range. Bhaud (1984) claims that the results of larval dispersal cannot be distinguished from such ecologic constraints. Notwithstanding this view, an analysis of the warm-temperate prosobranch fauna of the southeastern coast of the United States (Beaufort, North Carolina) shows that species with non-planktonic development are with few exceptions constrained largely to a limited length of the continental coastline and are all restricted in geographic range to the western Atlantic. Excepted are three species presumed to have been introduced to the eastern Atlantic on oysters. In contrast, those species from the same region known to have teleplanic veliger larvae are all shown to have wide latitudinal ranges in the western Atlantic (some over 60°) and 81% are amphi-Atlantic in their geographic distribution. These data are set forth in more detail elsewhere.

Any consideration of the contemporary distribution of species must also account for the

Fig. 3 Distribution of teleplanic gastropod veliger larvae in the epipelagic of the tropical Pacific Ocean. Data from 337 plankton tows. Arrows show surface circulation generalized from pilot charts. Distributional data for the central Pacific in part from Scheltema (in the press, 1986) with the addition of 127 previously unreported locations. Symbols as in figure 2.

Table I Larvae of sublittoral Gastropoda common in the epipelagic waters of the tropical Pacific Ocean (Based on 337 stations)

TAXON	No. Stations	Percent Occurrence
All Gastropoda	240	71.2
Architectonicidae	124	36.8
Naticidae	83	24.6
Cymatiidae	82	24.3
Neritidae	52	15.4
Cypraeidae	37	11.0
Thaididae	29	8.6
Triphoridae	27	8.0
Coralliophilidae	22	6.5
Bursidae	20	5.9
Tonnidae	18	5.3
Strombidae	16	4.7
***Other**	176	52.2

* Includes Cassidae, Columbellidae, Cerithiidae, Turridae, Ovulidae, Conidae and Muricidae each at less than 3% of stations Data from the central Pacific (Scheltema, in the press, Table 2) to which has been added 127 additional samples from the eastern and far western Pacific.

dimension of time. Events that affect species distribution may be in the order of decades, centuries, thousands of years, or over geologic periods of time. Examples are:

a) climatic change which affects the latitudinal range of species (e.g., Bousfield & Thomas, 1975 describe changes in the Virginia fauna since the Early Hypsithermal, ca. nine thousand years ago);

b) transgression and regression of sea level (Vail et al., 1977) which alter the amount of available habitat along coastlines and the number of "stepping stones" available for dispersal;

c) the opening and closing of seaways or corridors which can restrict or facilitate the possibility for dispersal (cf. Hallam, 1973);

d) seafloor spreading which over geologic time affects the size of ocean basins that act as barriers to the dispersal of coastal species.

The closing of seaways and corridors markedly affected the possibility of larval dispersal during the Tertiary. The Tethys Sea and the passage between North and South America provided a continous circumtropical route by which larvae could have been transported westward between the tropical Indo-Pacific and Atlantic Ocean (Fig. 5). Likewise, the corridor between North and South America allowed a connection between the tropical marine faunas of the western Atlantic and eastern Pacific. The Tethys Sea closed at its eastern end at the beginning of the Oligocene (ca. 36 million years ago) thereby separating the tropical Indo-Pacific and Atlantic faunas, but there still remains a large number of families and genera of molluscs in common between the two regions, reminiscent of a former seaway connection. The corridor between North and South America closed in the Early Pliocene (ca. 3 million years ago) preventing the possibility of any larval exchange between these two regions, but the period is short enough so there still exist some species of molluscs held in common between the western Atlantic and eastern Pacific.

The mode of development of Tertiary fossil prosobranch gastropods can be inferred from the

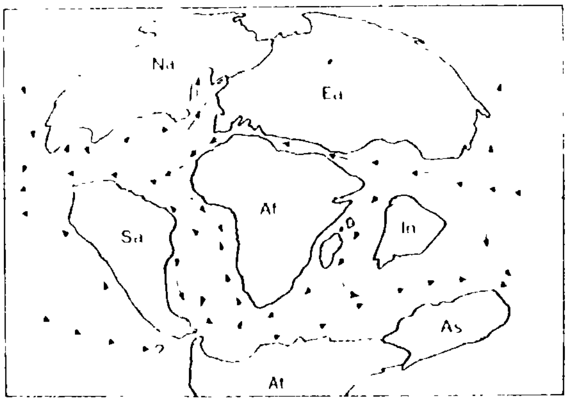


Fig. 5 The disposition of continents and the inferred surface circulation of the World Oceans during the Cretaceous/Paleocene (65my ago). Arrows show surface circulation. Na= North America, Ea= Eurasia, Sa= South America, Af= Africa, In= India, At= Antarctica, As= Australia. (After: T. H. Van Andel, Fig. 12, 1976: 18; data from: Dietz & Holden, 1973, continental position; Berggren & Hollister, 1974; Luyendyk et al., 1972, circulation pattern).

protoconch or larval shell at the apex of well-preserved and identifiable juvenile or adult specimens (Jablonski & Lutz, 1983; Scheltema, 1979; 1981; Shuto, 1974). From what is known about congeneric or confamilial forms, it is also possible to distinguish which species have teleplanic larvae. Such knowledge makes inferences possible about larval dispersal in the geologic past.

Seafloor spreading in the Atlantic during the Tertiary has resulted in the ever-increasing distance between the African continent and Central and South America to the west. It is estimated that if allowance is made for the higher current velocity (Luyendyk et al., 1972) and also the smaller size of the Atlantic Basin during the Early Tertiary (Fallow, 1979; Fallow & Dromgoole, 1980), the time required to cross from Africa to the Caribbean by a passively drifting larva would have been between ca. two to four weeks, well within the lenth of the development for most contemporary species with planktotrophic larvae (Scheltema, 1979). Today the time required is substantially greater, between two and six months (depending on the current system considered) and the Atlantic, because of its now greater width, acts as a filter allowing only the passage of some teleplanic larvae.

Ekman (1953) proposed that the eastern Pacific acted as a barrier to larval disperal. Thorson (1961) believed that "under average conditions even long-distance larvae have a much too short pelagic life to survive the critical distances across the eastern Pacific...." Zinsmeister & Emerson (1979) discuss the possibility of larval dispersal across the eastern Pacific Barrier and conclude that the relative paucity of Indo-West Pacific species of molluscs in the eastern Pacific is owing to the "vast expanse of open water" and "lack of suitable habitats with available ecological niches ...." Leis (1984) examined the possiblity of larval dispersal to explain the high Indo-Pacific element of coral reef fish that occurs in the east tropical Pacific (up to 24%), but was unable to arrive at a definite conclusion owing largely to insufficient plankton data. The distributional data of architectonicid and cymatiid veliger larvae (Fig. 3) show a decrease in their occurrence between 100° and 160°W and suggest that the East Pacific may also serve as an efficient filter for dispersal of many gastropod species.

The Mollusca of central Pacific islands represent an attenuated Indo-Pacific fauna and the endemism, even of the more remote Hawaiian Islands, is relatively low (ca. 20% Kay, 1979) compared to terrestrial insects among which some taxa may have 98% endemism (Carlquist, 1974). Owing to the geologic origin of tropical central Pacific islands by volcanic activity from the ocean floor, colonization by sublittoral gastropod species necessarily must have resulted from long distance dispersal (Scheltema & Williams, 1983). Taxa without larval development generally are absent from Polynesian Islands (e.g. Volutidae, Cancellariidae, etc.). The widespread persistence of Indo-Pacific species on central Pacific islands suggests that there is at least intermittent gene flow among island populations and also between them and other regions of the Indo-Pacific. To test such an hypothesis, examination of genetic variation of specific gastropod species is now required (see: Slatkin, 1985) along with data on the larval dispersal of such species. The latter depends on the description and subsequent identification of the larvae.

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BIOGEOGRAPHY OF OCEANIC ZOOPLANKTON

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INTRODUCTION

Distribution of marine zooplankton has been discussed in recent years by a number of authors, e.g. Van der Spoel & Pierrot-Bults (1979). The absence of effective geographical barriers and the paucity of ecological niches in the ocean, as already pointed out by McGowan (1971), and the slow process of allopatric speciation are accountable for the low number of species in oceanic zooplankton. This paper, by examining the distribution of some pairs of morphologically similar species, proposes a hypothesis that a unique type of speciation of planktonic animals in the sea may sporadically take place in an area where stability of oceanic condition is altered by the admixture of waters from different origins.

DISTRIBUTION PATTERNS AND ANALOGOUS SPECIES

It has long been noted that general distributional patterns of oceanic zooplankton coincide with large-scale closed and semiclosed oceanic structures. Beklemishev (1971) and McGowan (1974), for instance, proposed distributional regions for the world ocean and the Pacifc respectively. Their proposals apperently show a high degree of parallelism (Table I). Most oceanic plankton live in more than one region and/or more than one ocean. In a survey of 952 species, Van Soest (1979) found that 502 species are widely distributed between 50°N and 50°S. Beklemishev (1981) noted that 90 out of the 100 species in his survey are found in the same type of regions in different oceans.

Identification of oceanic zooplankton is generally based on morphological characters. When samples of a species from different parts of the world ocean are compared, trivial but consistent morphological differences are sometimes noted in different geographical populations of so-called cosmopolitan or widely distributed species. These morphological forms are designated at some taxonomic level from geographical forms to distinctive species, usually at the discretion of the authors. It is interesting to note that the distribution of these variations exhibits typical geographical patterns. Van Soest (1975) reported latitudinal morphological variations in some salp species. Van der Spoel (1967; 1976) showed that different formae are usually found in different water masses. Shih (1986) regarded those morphological variations which are distributed in similar latitudes in the same or different oceans as analogous species, referring to their similar morphology and parallel distribution, and gave several examples of oceanic copepods. Most analogous species are epipelagic and found in equatorial to central waters (Shih, 1979).

There are two types of analogous species: interoceanic and intraoceanic. Interoceanic analogous species have each species of the pair living in a different ocean. Usually they are distantly separated from each other by a continent but sometimes they are close. Several pairs of interoceanic analogous species have one member found in the South Atlantic and another in the Indo-Pacific. For instance, the amphipod crustaceans *Phronima colletti* (Atlantic) and *P. bucephala* (Indo-Pacific), the chaetognaths *Sagitta serratodentata* (Atlantic) and *S. pacifica* (Indo-Pacific), and the copepod crustaceans *Pontellina plumata* s.l. with Atlantic and Indo-Pacific forms. The western boundary of these Indo-Pacific taxa usually lies south of Port Elizabeth. The eastern boundary of their Atlantic counterpart is generally located south of Cape of Good Hope but occasionally extends to the coastal water off southeastern Africa, sometimes to Durban. The combination of the African continent and the Agulhas Current system seems to be an effective geographical barrier to members of these pairs of analogous species (Shih, 1986).

Table I Zoogeographical regions of marine zooplankton according to Beklemishev (1971) and McGowan (1974).

REGIONS		
ALL OCEANS (BEKLEMISHEV,1971)	**PACIFIC (MCGOWAN,1974)**	**CHARACTERISTICS**
Primary oceanic cyclic communities	**Subarctic & Subantarctic, North & South Central, & Equatorial provinces**	**Large-scale oceanic gyres, recirculation present**
Secondary oceanic terminal communities	**North & South Transitional provinces**	**Transitional zones between large-scale gyres; strong east west currents present**
Secondary distant-neritic terminal continental communities	**Eastern Tropical Pacific province**	**Area between large-scale oceanic gyres and coasts; medium-scale & stable eddies present**

Several pairs of intraoceanic analogous species are found in McGowan's Eastern Tropical Pacific province. Each pair contains one species widely distributed in the tropical and subtropical Indo-Pacific and another limited to the eastern Pacific, with an overlap in the latter region, e.g. the chaetognaths *Sagitta pacifica* (Indo-Pacific) and *S. bieri* (E.Pacific), the copepod crustaceans *Pontellina plumata* (Indo-Pacific) and *P. sobrina* (E.Pacific), and the amphipod crustaceans *Phronima stebbingi* with Indo-Pacific and East Pacific forms. The oceanography of the eastern tropical Pacific is complicated by a strong upwelling system and the convergence and divergence of several oceanic currents as well as by the O_2 minima (Wyrtki, 1967). The coexistence of both members of analogous species in this unstable oceanic environment does not conform with the general belief that speciation requires geographical separation or other isolating mechanisms.

PLANKTOPATRIC SPECIATION - A HYPOTHESIS

Oceanic planktonic animals are sometimes found outside their normal range of distribution because they are frequently carried away by oceanic currents or other moving water bodies. Wiebe & Boyd (1978) and Boyd et al. (1978) reported the deterioration of populations of the western North Atlantic Slope Water euphausiid, *Nematoscelis megalops*, entrapped in Gulf Stream cold core rings when the cold core waters of the aging rings gradually assumed the biological and physical characteristics of the surrounding Sargasso Sea. Tumantseva (1981) recorded the change of planktonic community structure in the aging upwelling water of the eastern Pacific. These reports clearly demonstrate how a population of a species and a community in an ecosystem may react to a changing environment. Matsuda (1982) examined changing environmental factors acting upon known physiological processes in some littoral and terrestrial animals, creating new regulatory genetic changes, and leading to species evolution.

In a "stable" environment, speciation cannot take place if there is no isolating mechanism to prevent gene flow between different populations. In a changing environment such as an eddy, a cold or warm core ring, a meander of a current, an upwelling, or an area of convergence and divergence, the biological and physical characteristics will change as the water travels from one area to another. These changes consequently modify the community structure and also alter the number and kinds of entrapped niches. If a population cannot adapt to the changing environment and find a niche, it will face elimination. If some individuals of a population can adapt to the new environment and find a new niche, they will survive and probably proliferate. Some individuals or segments of a population possessing unusual alleles that were repressed in the original environment may develop in the new environment in a separate niche. As a consequence reproductively isolated populations may become established. This type of species formation probably does not fit any particular mode of speciation described in the literature and is here termed planktopatric speciation which seems only to apply to oceanic plankton.

CONCLUDING REMARKS

Our knowledge of biogeography of oceanic zooplankton is mainly limited to the epipelagic species. The general patterns of distribution of these animals are highly correlated with those of the major water masses and current systems (Beklemishev, 1971; McGowan, 1971). While water masses are the major biogeographic units in the ocean, the mixing of water between different water masses is a recurrent event. In areas where the mixing is pronounced, e.g. rings and eddies formed in the western boundary currents (Backus et al., 1981) and the centre of convergence and divergence in the eastern tropical Pacific (Wyrtki, 1967), individuals of a population or a community are frequently entrapped in the migrating water and subjected to the change of their immediate environment. These moving hydrographic structures are therefore evolutionary laboratories of nature. With the high frequency of mixing in some parts of the oceans and with the possibility (probably very insignificant) of the expression of new gene complexes of a population in a different environment, planktopatric speciation may take place. The hypothesis of planktopatric speciation may explain the coexistence of both members of several analogous species pairs in the eastern tropical Pacific where mixing of waters from different origins is most thorough and an isolating mechanism is apparently lacking.

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WHAT IS UNIQUE ABOUT OPEN-OCEAN BIOGEOGRAPHY; ZOOPLANKTON ?

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INTRODUCTION

Speciation and distribution are frequently considered to differ in the pelagic environment when compared to the terrestrial one. These differences are explained by the absence of barriers, the three dimensionality of the oceans, the effect of currents making dispersal a long term phenomenon and the floating behaviour of organisms. In this paper special attention is given to the last phenomenon.

In 1887 Victor Hensen defined (zoo)plankton as (animals) passively drifted about by water movements (Hensen, 1887). Does this passive drifting determine dispersal and distribution. Is the unique character of zooplankton related to its behaviour in space and time? If we have to answer this question negatively the biogeography of plankton is no longer unique, but probably the definition of plankton is incorrect.

Many examples are known of different species showing, in one current system, different patterns; sometimes, for example, two allopatric (geographically, horizontal as well as vertical, separated) species are sympatric with a third species although all three are dependent on the same current system (Van der Spoel & Heyman, 1983). This seems to contradict the hypothesis that passive floating directly determines distribution. Some species are known to be transported by one and not by another current, therefore passive drifting does not, on its own, determine dispersal. "Passively drifted about" certainly contributes to dispersal of specimens but seems not to contribute to dispersal of populations and distribution, consequently not to a unique biogeography.

The three-dimensionality of the environment of marine plankton is typical but essentially not unique as it is also the environment of nekton and is found in the limnic environment, in soil and in the tropical rainforest. In the open ocean the three-dimensionality is only more marked than elsewhere.

Zooplankton lives in seawater, a constantly mixed and extremely large substrate without abrupt changes in conditions like found in terrestrial environments. A normally vertically migrating zooplankton species will in the area that it comes from, meet no greater changes in most conditions than if it were to migrate horizontally across all oceans. If this special character of the environment induce the uniqueness of open-ocean zooplankton distribution, then it has the same consequences for nekton, for phytoplankton, and probably to a lesser degree, also for benthos. But does not the present conference combine plankton and nekton precisely because they both show the same typical phenomena?

TWO POSTULATES

With regard to the large area available we should realise that distribution is not only the result of the environment, of the seawater and its basins, but also of the expression of life; thus distribution develops by interaction between the influences of the environment and the behavioural and physiological expression of life as it is fixed in genetic structures. Within the range of a taxon there is harmony between animal and environment; outside it there is conflict. "Arguments" maintaining this conflict may be raised by the environment, by the organism or, as is usually the case, by both at the same time.

As a first hypothesis it is here postulated that "in plankton it is not the influences of the environment but the characters of the organism that chiefly determine the range of a species ". This makes the biogeography of plankton and nekton unique. Translated into biological terms it means that population dynamics restrict the dispersal and distribution of species to a relatively small area, smaller than the niche which is available if a.o. drifting were to controle distribution (cf. Angel, this volume; Katona, this volume). Mayr (1967: 201, 468) summarized the adaptations of taxa which enables them to utilize more of the available niches, and as a consequence accepts the incomplete occupation of a niche when population dynamics are not fully adapted.

The biogeography should be studied with the clear understanding that its is different from ecological biogeography (Mayr, 1982). The population density, the number of specimens per unit of space, is not considered at this place, rather, the geographic space occupied by the total of populations of a taxon. Superimposed on the fluctuation of the geographic size of populations are, of course, the usually sinusoid density and population structure fluctuations (Voronina, 1978). The above hypothesis can only be accepted if it is coupled with an explanation of why the process of evolution did not succeed in developing species that can occupy the total area available to them.

The total available area is considered to be the entire ocean, or that section of it without relative sharp discontinuities in environmental factors. In cases where population dynamics restricts the occupied area it is e.g. reproduction, mortality, maximum distance permitted between specimens and individual movement behaviour which restrict distribution and which, therefore, did not adapt "optimally" during the process of evolution. Or should we say adapt "maximally"? Could it be profitable to be unable to occupy all of the available area?

Adaptations are usually not maximal when they are optimal because "optimal" still entails response to fluctuating environmental conditions (Mayr,1967). For plankton, is the size of the available range also a fluctuating condition? This hardly seems to be the case, since the conditions in the ocean and ocean size do not change strongly, not even in terms of geological time. Conditions, expressing themselves as fronts or barriers, which by fluctuating keep ranges smaller than possible are not expected to be limiting either. One strongly fluctuating condition is the available nutrient concentration at higher latitudes, in seasonally mixed waters and in near-shore areas. However, this fluctuating condition directly influences the populations and not the geographic size of the ranges.

A breakdown of the gene pool when the range becomes very large, when the entire available space is occupied, can in general be rejected as an explanation of restricted ranges as there are many species, oceanic as well as terrestrial, with very large distributions which one still recognize as good species.

A solution adopted here is to accept a second hypothesis: "Evolution in the pelagic environment (in large populations) is too slow to reach optimal adaptation to the conditions of the large area available, resulting in smaller ranges than possible". Or environmental changes are still too quick which is the same as evolution is too slow.

Though the ranges are smaller than the available space, the individual populations may be extremely large. In these large populations, changes of the gene pool are difficult to achieve. It must be clear that a relatively small number of large populations in a range also depresses rates of evolution. Slow evolution implies not only low speciation rate, inperfection of adaptation to specific conditions and great potential flexibility of the gene pool, but also little tendency for new genetic adaptations resulting in new ranges. With the great flexibility of the gene pool, the within population flexibility is meant. It is visible in many species as temporary ecological adaptations, polymorphism or polytypism.

A MODEL

In figure 1 a dynamic model of the major factors determining population- and range-size is given for three species I, II and III considered to be in an equilibrium state (RANGE IN EQ. STATE). The effects of population dynamics, evolution and environment are demonstrated here successively. In figure 1 as well as 4 the ranges are pictured as

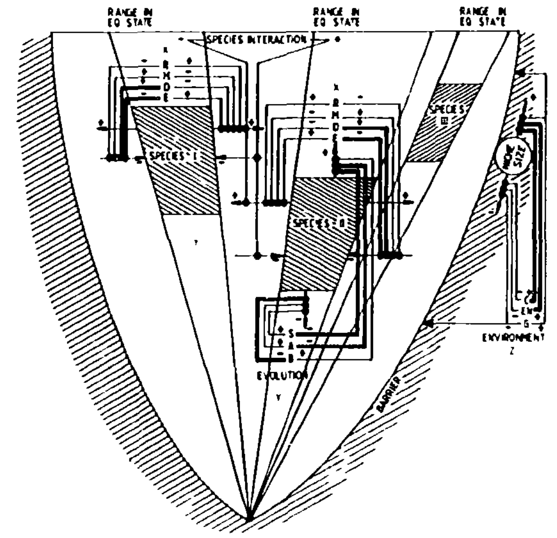

Fig. 1 Dynamic model of plankton ranges of three species: I, with the influences of population fluctuations; II, with niche size fluctations; and III, showing the influences of population dynamics, evolution and environment. The populations are grouped to show the influence of population dynamics as horizontal, and those of evolution and the environment as vertical shifts in the space available between barriers. A= local adaptations, B= new radiating adaptations, C= climate influences, D= expatriation, E= max. effective density, EN= environmental influences, EQ= equilibrium, G= geomorphological effects, M= mortality, R= reproduction, S= speciation, X= population dynamics, Y= evolution effects, Z= environmental effects, += increase, stimulation, -= decrease, limiting, ——→ = vector of influence, or dispersal.

transformable quadrangles which may shift up and downwards in the available environment that becomes smaller at the underside and wider at the upper side of the model depicting in that way the effects of environmental factors. The vertical shift is depicted as determined by effects of evolution and the size changes due to population dynamics are depicted as broadening and narrowing of the quadrangles.

For species I in figure 1 the major factors of population dynamics are pictured as reproduction (R), mortality (M), drifting of specimens out of the range (D), and maximum density of organisms for effective mating (E). More reproduction (+), less mortality(-), and larger maximum distances allowed for effective mating (+) will result in population increase. However, in plankton the result is also range enlargement (+): the specimens move at random so that abundance (=concentration) drops in favour of range enlargement (=dilution). In plankton, drifting is usually very strong (+); specimens find each other as a rule by accident, so that nevertheless small distances are required (-) between individuals. This has the effect that populations and ranges of populations tend to stay relatively small (-). Species interaction in plankton, indicated in figure 1, is never reported as an important phenomenon (cf. McGowan & Walker, 1985), perhaps not only by the fact that it is difficult to document.

Evolution changes the species so that it may live elsewhere in space or time; this can also be expressed as 'evolution alters the niche for a given line of descent.

The effects of evolution on plankton are indicated with species II. When the range stays smaller than the area available, evolution is stopped or slowed down, so speciation (S) is at a low level (-), adaptation to specific local conditions (A) is small (-), genetic flexibility stays high so that the available niche (arrow on top of species II) stays or becomes larger (+). New genetic adaptations, e.g. in peripheral populations or founder populations are not developed (-) so that no new ranges, indicated by the lower arrow (-) are populated.

Effects of selective pressure in plankton are slowly realized as the population size is very large in general ("A" stays small). In populations with high abundance genetic drift tends to create a large percentage of homozygotes, thus tending to reduce radiation and diversity. However. even in these large plankton populations this reducing effect is not realised, and probably only the formae of species (Van der Spoel, 1971) can be explained by this effect, though the genetic drift must be large (as "D" is large).

In plankton, moreover, the environment (depicted at the right side in Fig. 1) is characterised by large, not sharply delimited climatic belts (C)(+) and gradual transitions in environmental conditions (EN)(+) which render larger (+) available areas. Geomorphology (G) does not present open ocean plankton with many barriers (-) so that the niches are in general very large (+).

In my view everything combines to make the available area larger and the population smaller, so that the second floats 'uncontrolled' in the first.

Comparing this with the dynamic model for e.g. terrestrial animals (Fig. 4), drawn along the same lines as that for plankton, great differences are obvious, even when only the factors are considered which were applied for plankton. Reproduction and mortality in terrestrial animals determine to a greater extent the range size than transport of specimens does, while species interaction by competition (+) frequently restricts the population (-). All other factors are, however, in favour of population enlargement (+). Evolution has gone much faster than in the sea and speciation (S) and adaptation (A) are both relatively frequent (+) which restricts niche size but not niche numbers while new adaptations (B) may enlarge the area into which a taxon splits off new populations. The geomorphology of the terrestrial environment, in particular induces small niche size, while climate and other environmental factors do not particularly enlarge it.

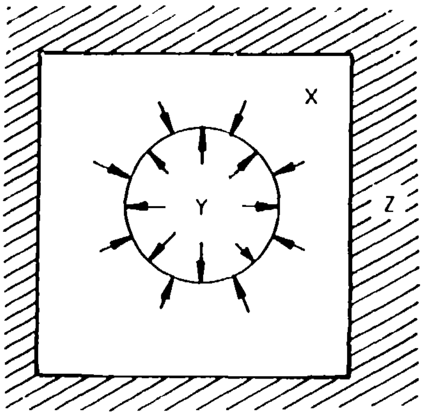

Fig.2 A plankton population range, not restricted by environmental vectors, but by population dynamics and evolution (for explanation see Fig.1).

CONCLUSION

As a conclusion one can state that zooplankton distribution (Fig. 3) is influenced not mainly by the environment, but by population dynamics which keeps ranges small. A lack of evolutionary specialisation towards narrow and specific environmental conditions makes the available range large. Therefore, it is almost logical to accept that: population dynamics and evolution keep the size of the actual range in a sort of equilibrium.

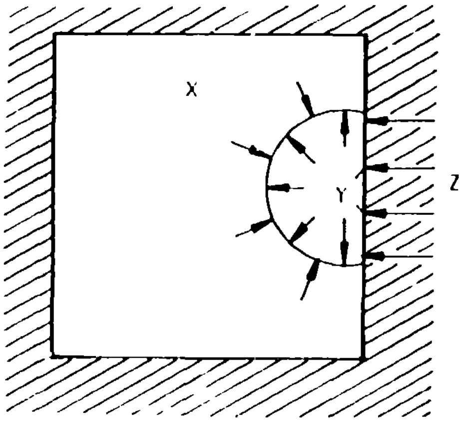

Fig.3 A plankton population partly restricted by environmental vectors and largely by population dynamics and evolution (for explanation see Fig.1).

In terrestrial animals (Fig. 4) just the reverse is found. The environment keeps the populations in a given space and speciation and adaptation, thus evolution, restrict the area available. Population dynamics alone may work to enlarge the range. Newly evolved adaptations may stimulate this too. Here environment and evolution keep the range in a kind of equilibrium while population dynamics fluctuates to get maximal profit out of this equilibrium.

Of course intermediate situations between the two are possible. In plankton the environment may have an influence (Fig. 5), but then, population dynamics also restrict the range. In terrestrial animals boundaries are known which

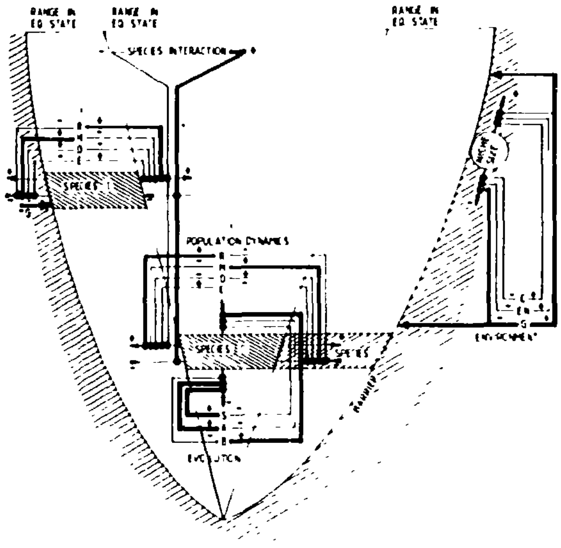

Fig.4 Dynamic model of non-plankton ranges of three species; I, with the influences of population fluctuations; II, with niche size fluctations; and III, showing the influences of population dynamics, evolution and environment, in the same manner as in figure 1.

are not induced by the environment or by species interaction (Fig. 6) but here primarily evolutionary effects, as distance barriers, restrict the range and the population dynamics do not do so directly.

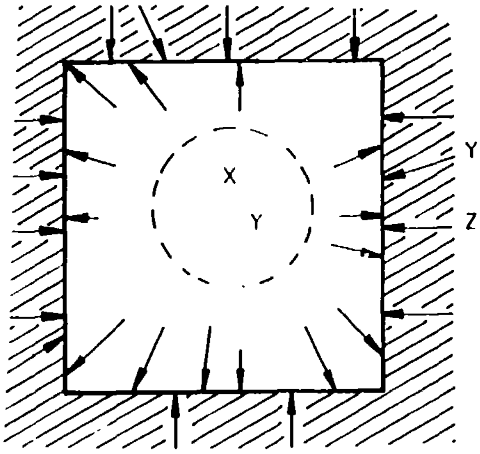

Fig.5. A non-plankton range influenced by evolution and population dynamics but limited by environmental conditions (for explanation see Fig. 1).

Accepting the extreme hypotheses given above, "population dynamics restrict ranges", "evolution is slower than on land" and "there is an equilibrium between population dynamics and evolution", speciation above species level will hardly be possible and distribution borders of taxa will usually not be congruent as they are determined by the individual species and not by a general external factor. This is exactly what is found in nature, evolution in the sea is slow, only 40% of all taxa live in the sea that covers 70% of the earth, so the rate in producing numbers of taxa is 4 times as slow as on land, and of the small number of taxa hardly any shows geographic speciation above the subspecies level. Usually adaptations are ecophenotypic, giving rise to varieties. It is logical that with decreasing number and increasing size of populations the evolution rate drops, no polytypy, no geographic races or subspecies can develop when there is a lack of separated populations. Also distribution limits are usually markedly different for species occurring in the same area or province (Fig. 7).

From figures 1 and 2 it is therefore clear that the uniqueness of zooplankton biogeography is induced by:

1. the effect on population dynamics, by drifting about of specimens, thus not directly by the displacement of specimens or ranges,

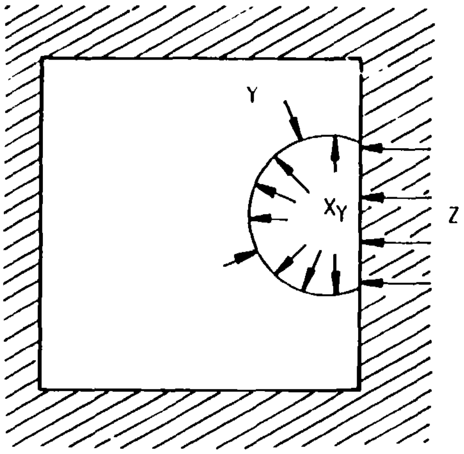

Fig.6. A non-plankton range influenced and partly limited by evolution processes but not by population dynamics (for explanation see Fig. 1).

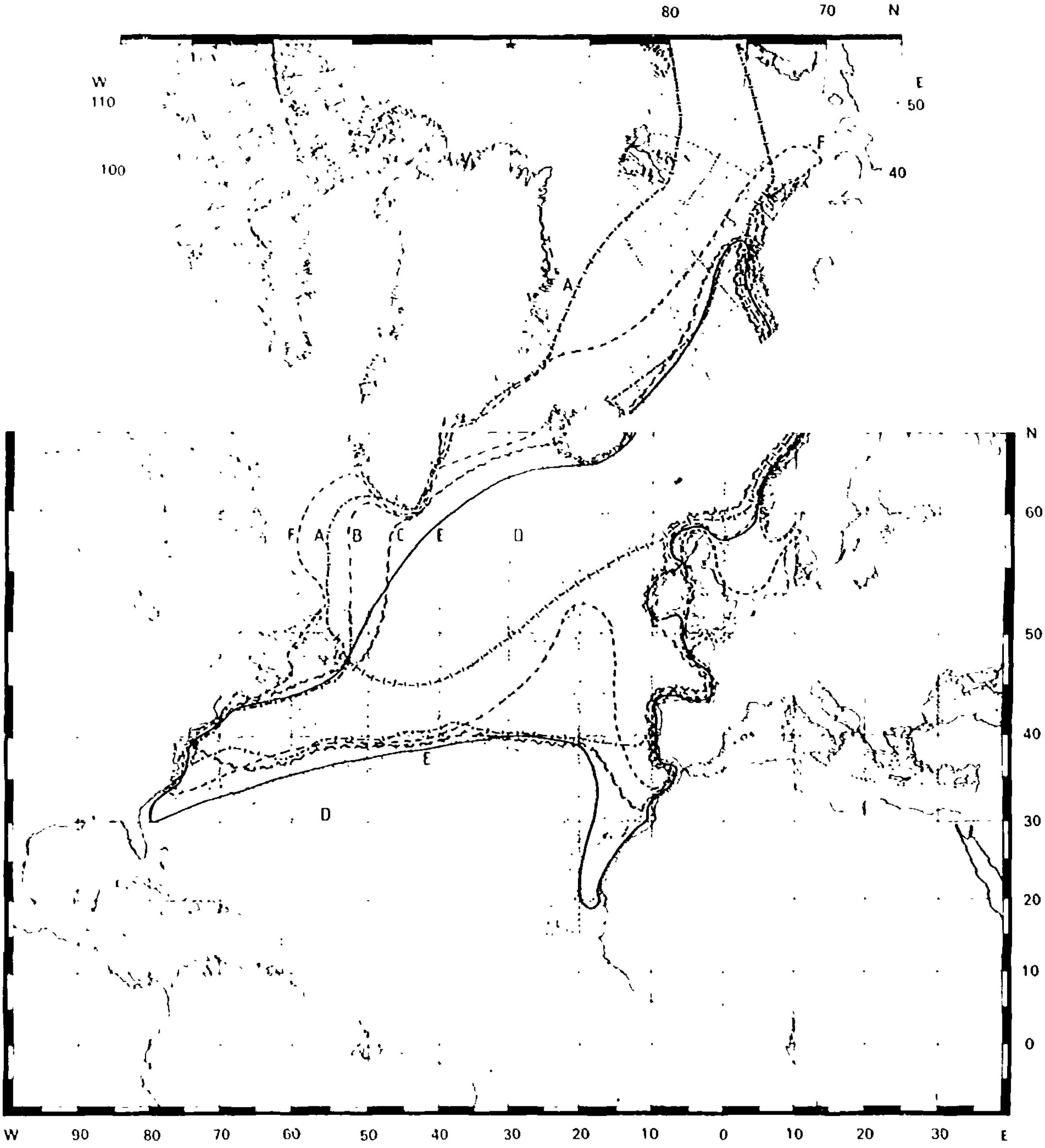

Fig.7. Ranges of North Atlantic Cold water taxa to show the non-congruency of ranges.
A= *Nitzschia cylindrica* ; B= *Clio pyramidata* forma *pyramidata* ; C= *Salpa fusiformis* coldwater form; D= *Calanus helgolandicus* ; E= *Sagitta tasmanica* ; F= *Limacina retroversa*.

2. slow evolution and low speciation rate (in very large populations which still do not fill the available area) in spite of local and temporary adaptations (ecophenotypes), are frequent,

3. the character of the sea: a large substrate without abrupt differences or changes.

As a final conclusion and working thesis, a new definition for zooplankton is proposed:

"Zooplankton comprises species whose specimens are passively drifted about by water movements within the stable range (defined by population dynamics) occupied by the (large, temporary or permanent) populations"

This definition makes it possible to apply normal biogeographical principles to planktonic taxa as the populations are stable units again (Mauchline, this volume). However, when a taxon by its own genetic characters can restrict its distribution in space, it can for the same reason restrict its distribution in time. This means that extinction is determined by the taxon itself, by its genetics, and explanations of extinction through catastrophes become unnecessary.

ACKNOWLEDGEMENTS

The anonymous reviewers are cordially acknowledged for the fine work they did.

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PATCHINESS AND THE PARADOX OF THE PLANKTON

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INTRODUCTION

Biogeography is the study of species ranges, concordance of species ranges and the factors which influence these ranges. One approach is to consider the species whose ranges overlap in some environment and investigate the mechanisms which facilitate their coexistence and which regulate their relative abundances. The major pelagic habitats support far more species than expected from the general ecological principle that competing species in an equilibrium system can not coexist indefinitely. Three types of hypotheses have been developed to explain the apparent coexistence of apparent competitors in apparently equilibrium ecosystems. Niche diversification hypotheses (Schoener, 1974) predict that similar species can co-occur because they have specialized to make use of diffent parts of the spatial or temporal habitat, thus reducing competitive interractions. Disequilibrium or disturbance theories predict that competitors co-occur because the ecosystem is not at equilibrium, but instead environmental fluctuations occur on such a scale as to prevent the ultimate exclusion of competing species (Hutchinson, 1961; Richerson, et al., 1970; Paine & Levin, 1981). Predation theories (Darwin, 1859; Caswell, 1978) predict that predation pressure either maintains the abundances of the prey species below the level of resource limitation, or occurs in a heterogeneous manner, thereby keeping the ecosystem in a state of disequilibrium.

DISCUSSION

We now have nearly twenty years of biological and environmental data from the diverse and stable ecosystem in the North Pacific Central gyre. We have used these data to test the predictions of the theories of niche diversification and disequilibrium/disturbance. Although the predation hyphotheses are appealing, they have not yet been formulated in a way that can be tested in the field and can not be considered further here.

Niche diversification theories predict that species abundance centers should be separated according to some predictable spatial or temporal structure in the environment. We have detected neither horizontal gradients nor seasonal cycles within the Central Pacific (Hayward et al., 1983). The primary environmental structure available is provided by the vertical gradients of light, primary productivity, nutrients, temperature, etc. McGowan investigated the spatial distributions of 123 species of copepods collected in 62 bongo net samples from six to eight depth ranges during a ten day period in August-September, 1968 (McGowan & Walker, 1979). Only seven patterns of vertical distribution were detected. The vertical patterns were stable horizontally, and were present in every survey between 1964 and 1969, regardless of season (Fig. 1).

The vertical distributions of more than 200 phytoplankton species were determined from seventy two samples collected by water bottles from eighteen depths at each of four stations during June, 1977 and August, 1978 (Venrick, 1982). Only two associations of species could be defined, one above 100-120m, the other below 75-90m. These appear to correspond to the nutrient-limited and light-limited regimes defined by Eppley et al. (1973). The chlorophyll maximum layer corresponds most closely to the region of transition between the two associations. These two associations are consistently present and were essentially unaltered by a major enrichment event that was observed in August, 1980 (Fig. 2). With neither zooplankton nor phytoplankton is there evidence that niche diversification has occurred among the species to

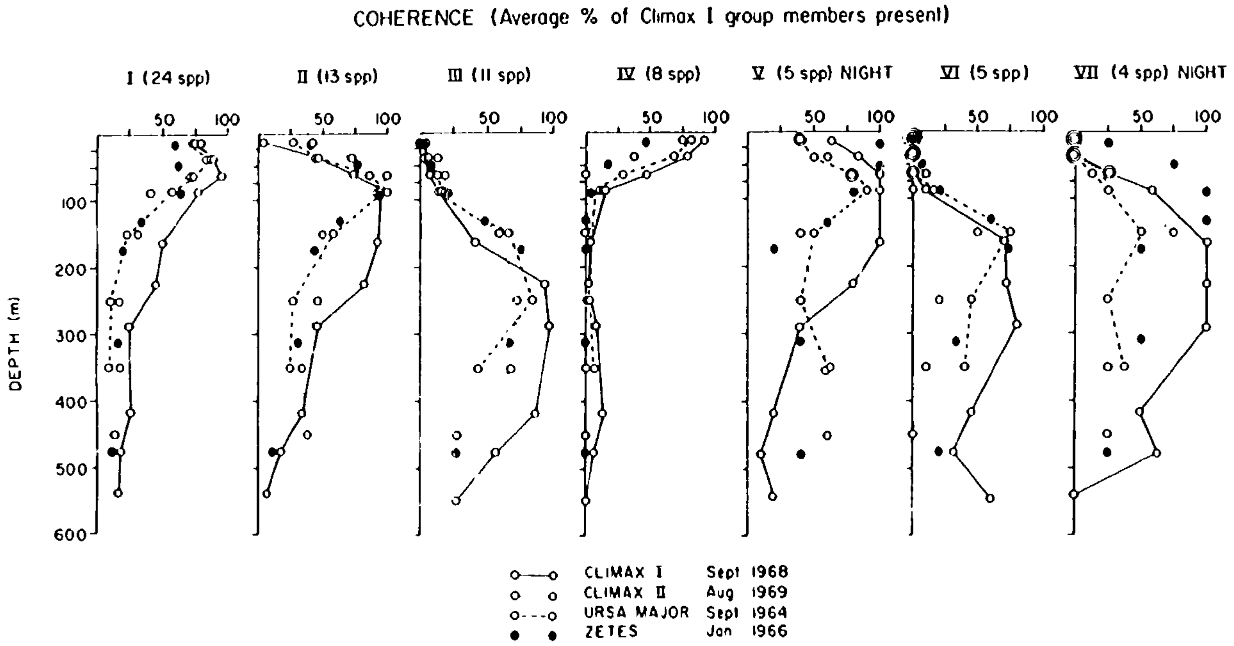

Fig. 1 Mean percent of the number of copepod species per recurrent group present (coherence) at different depths, on four cruises. Groups were defined on the basis of the 1968 data. For groups V and VII, the members of which are vertical migrators, only night data were used. For other groups all times of day were combined (McGowan & Walker, 1979; Fig. 17).

the extent neccessary to explain the persistent co-occurance of the large numbers of species observed. One might postulate that niche diversification among zooplankton takes the form of behavioral diversification rather than environment partioning. To the extent that this is true, the failure of niche diversification hypotheses is better illustrated by the phytoplankton which have a very limited range of "behaviour".

The disequilibrium/disturbance theories predict that, at some scale in space or time, rare species should become abundant. The scales postulated for these environmental fluctuations vary from small scale, short term disequilibrium fluctuations in the pelagic ecosystem (Hutchinson, 1961; Richerson et al., 1970) to the massive, long lasting disturbances of tropical forests, coral reefs and intertidal communities (eg. Paine & Levin, 1981). McGowan has used several analyses to test these hypotheses using abundance data of 175 copepod species collected during nine cruises over a 16 year period including three expeditions which traversed major portions of the Central Pacific. On no scale of space or time did any of the more than 100 rare species become abundant (Fig. 3).

Phytoplankton data have also been examined against the predictions of disequilibrium /disturbance in two separate studies. Under the assumption that congeneric species are most likely to be competitors, the data from 1977 and 1978 were restricted to congeneric species pairs (Venrick, 1982). There was no evidence that congeners co-occurred less often than expected were they distributed independently. Indeed, the tendency was in the opposite direction. Furthermore, among the congeneric pairs in the upper association, there was a tendency for the abundances to be positively correlated. Neither observation is consistent with predictions of disequilibrium theories.

The predictions of the disturbance hypothesis were tested by comparing the phytoplankton collected during 1977 and 1978 with that collected during the enriched period of 1980

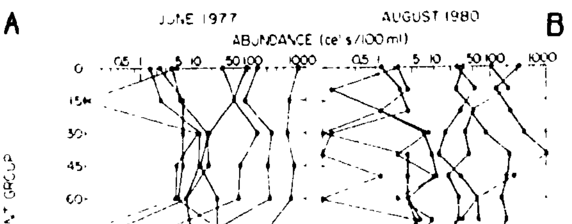

Fig. 2 Vertical distributions of species in the first two recurrent groups of phytoplankton species defined from data collected in 1977 and 1978. A. Mean abundances in 1977 (n=3). B. Mean abundances in 1980 (n=2).

(Venrick, in prep.). A total of 301,339 cells/m^2 were enumerated in 1980. This compares with 214,520 cells/m^2 in 1977 and 195,981 cells/m^2 in 1978, a mean increase of 47%. There was no detectable change in the rank order of species abundances. Nor was there any evidence that the rarer species increased more frequently than the abundant ones. Except for the increase in biomass, the phytoplankton associations were virtually unchanged. Among neither zooplankton nor phytoplankton is there evidence that rare species ever become abundant as predicted by disequilibrium/disturbance theories.

The strength of our results lies in their consistency. Observations on two very different types of organisms, collected by different techniques and on different scales, and analyzed independently produce the same results. For neither group of organisms do we find convincing evidence that processes of niche diversification or of disequilibrium/disturbance are responsible for the maintenance of species diversity in the North Pacific Ocean.

CONCLUSION

Taken as a whole, our results underscore the gap between the concepts of classical ecology and the reality of the pelagic ecosystem. The problem is two-fold. The first is historical. Modern ecology has its roots in the natural history observations of the past. Of necessity, these were observations of accessible and visible ecosystems. The tenents of modern ecology have been formulated for ecosystems with physical structure: structure in the sense of trees and rocks and rabbit holes; structure that can be hidden in and nested upon and eaten. Few theoreticians have focussed their attention on the relatively unstructured, pelagic communities.

At the same time, the traditional tools available to test the theoretical predictions are not available to pelagic biologists. We can not observe the system directly; we can not observe species ambits and interactions, but must infer them. We can not manipulate the system, translocate individuals, remove individuals, or exclude individuals from a portion of the system. Thus, pelagic biology does not produce the sorts of ecological observations that have traditionally tested and directed theoretical formulations.

If we are to procede toward understanding the regulation of community structure in the pelagic ecosystem, this gap between theoretical and pelagic ecology must be closed. We need to know the specific predictions of community regulation models for the pelagic ecosystem. We need to know, for instance, on which scales of space and time disturbances are likely to be effective in preventing competitive exclusion, how large the resultant abundance fluctuations will be, and how many species can indefinitely co-occur under the disequilibrium/disturbance models. We need to

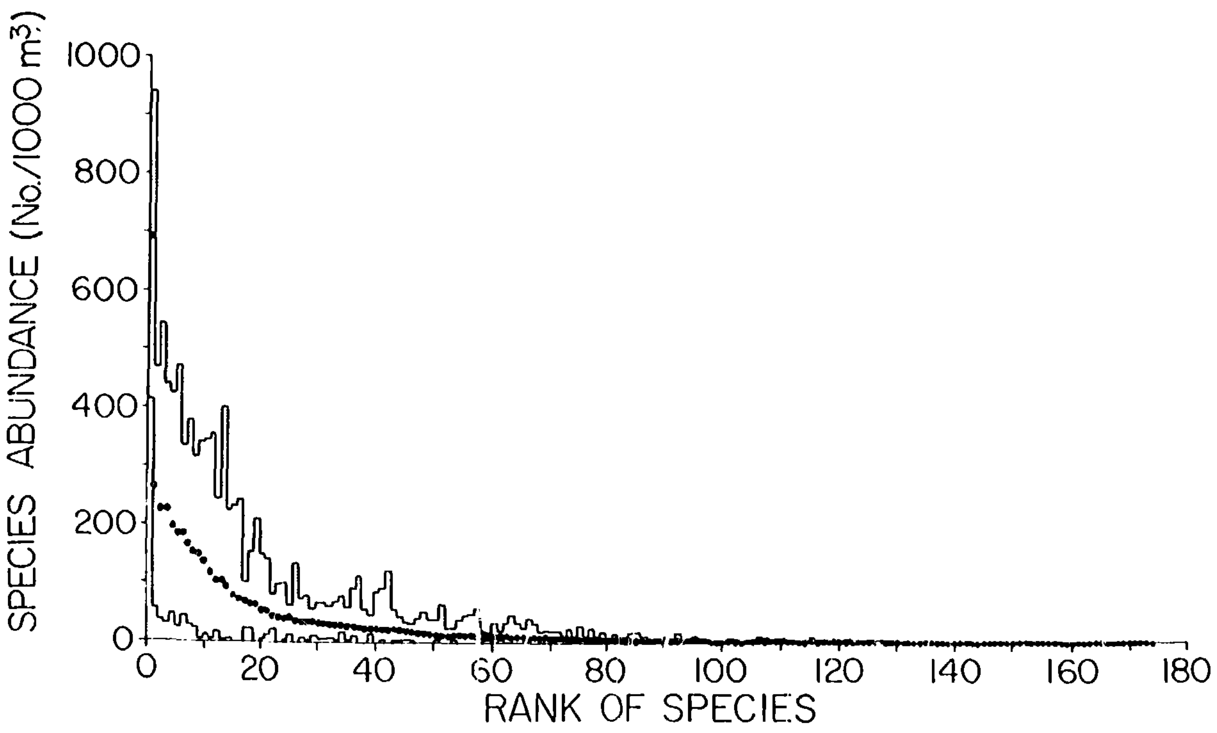

Fig. 3 Abundances of copepod species. Data points are the means of seven cruises : Jan. 1966, Sept. 1964; Sept. 1968; Aug. 1969; Oct. 1971; June, 1972; Feb. 1973. Grey bars indicate the range of abundances (McGowan & Walker, 1985; Fig.3.).

know the specific characteristics of predators which lead to predation enhanced prey diversity. For our part, we must attract the attention of theoretical ecologists by providing data from pelagic ecosystems which are suitable for testing the predictions of their models, thus presenting clear documentation of the apparent failings of their theories in pelagic systems.

ACKNOWLEDGEMENTS

This work was supported by the Office of Naval Research and by the Marine Life Research Group of Scripps Institution of Oceanography. I am indebted to John McGowan, without whom none of this work would have been accomplished, and to two perceptive reviewers who recognized that the primary purpose of this paper is to provoke thought, discussion and argument. I apologize for ignoring the intriguing 1981 model of D.Tilman (Am.Nat. 116: 362-393); this was due more to lack of space than lack of interest.

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TRANSITION ZONES AND SALP SPECIATION

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INTRODUCTION

Salpidae (Tunicata, Thaliacea) are widespread over all the ocean. Some species are almost cosmopolitan, for instance *Salpa fusiformis*, *S. maxima*, *Iasis zonaria* and *Thalia democratica*. Some species which are less eurythermous do not occur in the Mediterranean (*Traustedtia multitentaculata*, *Weelia cylindrica*). There are species whose distribution area is confined to the tropics of the Indian and Pacific Oceans (*Helicosalpa younti*, *Ritteriella picteti*).

At last there are species with a very restricted distribution area, for instance *Salpa thompsoni* having a circumpolar distribution in the antarctic and subantarctic and *Salpa gerlachei* occurring only on the western edges of Antarctica (cf. Van Soest, 1975a: Table IV).

In some cosmopolitan species (cf Van Soest, 1975a: Table III) the number of muscle fibers is variable. For example, *Salpa fusiformis* shows a high number of muscle fibers in the temperate watermasses and a low number in the tropical/subtropical parts of the oceans in both the Atlantic and the Indo-Pacific. This demonstrates biantitropical clinal variation going from high numbers of muscle fibers at high latitudes towards low numbers of muscle fibers at low latitudes.

CLINES AND SPECIATION.

These biantitropical patterns might be smooth clines, a gradual decrease in the number of muscle fibers going from high latitudes towards low latitudes, or stepped clines (sensu Huxley 1939): in one or more points in the cline there is a sudden drop in the number of muscle fibers (the step). When we are dealing with a stepped cline investigation of the transition zones or boundaries might give indications for phenetic and/or genetic differences between the demes living on both sides of the step in the cline.

Material collected by the Amsterdam Mid North Atlantic Plankton Expeditions (1980-1983) proved to be very suited to show the nature of these clines in more detail. Stations were made at relatively short distances and along a North-South transect at approximately 30° West in the North Atlantic, ranging from 55°N to 25°N (Fig. 1). Samples were taken at discrete depths: 0-50m, 50-100m, 100-200m, 200-300m, 300-400m, 400-500m, 500-1000m and occasionely down to 2000m, in the four seasons of the year. Subarctic water, Polar front, North Atlantic Drift, Temperate water, Subtropical water, Sargasso Sea water, Canary current and below depths of 800m deep Mediteranean outflow, Arctic and Antarctic intermediate water were

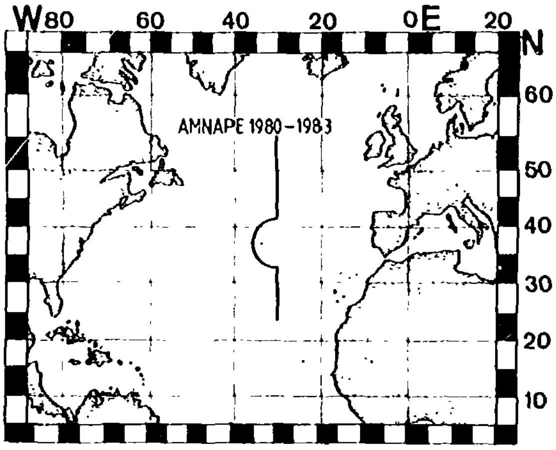

Fig. 1 The transect of the Amsterdam Mid-North Atlantic Expeditions.

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*) AMNAPE proj. 101A rep. no. 24 supported by a grant of the Netherlands Ministry of Education and Sciences.

sampled (see Van der Spoel 1981, 1985 ; Van der Spoel & Meerding 1983).

Salpa fusiformis has been investigated closely for the spring 1980 samples. It shows a stepped cline with a high number of muscle fibers north of 38°N and a low number of muscle fibers south of 38°N, these low numbers being the same as numbers previously reported by van Soest (1972) for the tropical Atlantic. In between, at 38°N at the step in the cline, intermediate numbers of muscle fibers are found (Fig. 2).

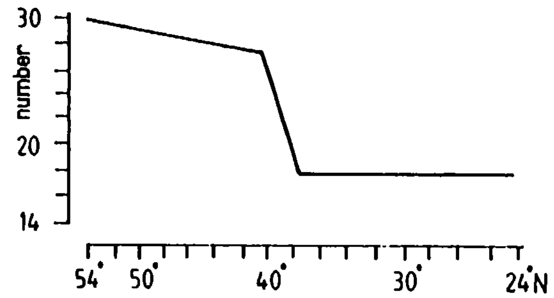

Fig. 2 Number of muscle fibers in *Salpa fusiformis* in the Mid-North Atlantic Ocean.

Population density and vertical migration show a variation related to the morphological variation. North of 38°N no clear diurnal vertical migration is found (Figs 3a & 3b). South of 38°N *Salpa fusiformis* does perform diurnal vertical migration. In night samples it is only found in the upper water layers (0-300m) while during the day it is restricted to the more profound water layers (300-1000m).

North of 38°N densities are very high, south of this latitude they are low. In between, in the area around 35°N the abundance is extremely low (De Visser & Van Soest, in the press).

There are also differences in the reproduction of both demes. North of 38°N the ratio oozoids/blastozoids is 1/10 up to 1/100. This points towards rapid growth of the deme by asexual reproduction and is reflected in the high density. South of 38°N the ratio oozoids/blastozoids is 10/1 and in part of the samples blastozoids are not even found.

The picture that emerges is that of two populations: a northern one with high muscle fiber counts, high population density in spring and a small ratio of oozoids/blastozoids, showing no clear diurnal vertical migration; a southern one with a low number of muscle fibers, low population density and a high ratio of oozoids/blastozoids, performing diurnal vertical migration. In between there is a low abundance but a restricted geneflow is in existence as their is evidence of interbreeding at 38°N. Material from other seasons is in preparation and does not conflict with the description of the populations mentioned above.

Muscle fiber variability in salps seems to be linked with the genotype of definite populations (cf. van Soest, 1975 b). These populations can, if genetic differences accumulate, become separate species, as might have fairly recently happened in the closely related *S. thompsoni* and *S. gerlachei*.

Allopatric speciation is not likely to have happened because complete isolation of populations in for example a tropical or Carribean warm water and a Mediterranean cold water population during, for instance, the Weichselien glacial is hard to imagine. In the southern hemisphere these processes are even more difficult to envisage.

True sympatric speciation is also ruled out

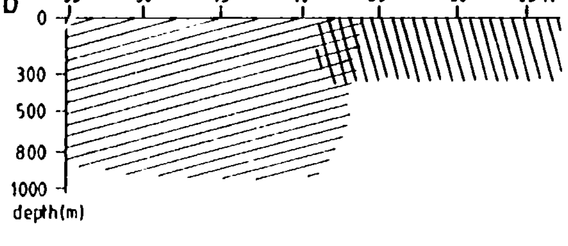

Fig. 3 Vertical distribution of *Salpa fusiformis* in the Mid-North Atlantic. a, daytime; b, night.

because adaptation to different ecological circumstances clearly exists along a North-South gradient. The small transition zone between the populations of *S. fusiformis* points towards clinal parapatric speciation, a speciation of two populations while maintaining geneflow. If the step in the cline becomes steeper an adaptive discontinuity may be reached which would result in two separate species (cf. Endler, 1977; White, 1978; Bush, 1981).

The step in the cline, associated with low population density enables the populations to build up genetical adaptations strong enough to distinguish them from each other.

Some kind of stasipatric speciation, possibly not visible because of clinal parapatric speciation, can also be involved. This presumes a chromosomal rearrangment favorable to selection mechanisms if homozygote but reducing fecundity when it appears in the heterozygote specimens. The difference with the clinal model of speciation is that the stasipatric one presumes a change in the karyotype which reduces fecundity in the heterozygote although the dimunition need not at all be complete. The clinal parapatric model of speciation presumes changes in genes (point mutations) which need not reduce fecundity in the heterozygotes. To see wether or not there are any chromosomal differences involved between the populations it is neccessary to study the karyotypes of these organisms The low population density in the vicinity of the step in the cline might point towards a reduced fecundity of heterozygotes.

Whether or not speciation related to the clines in muscle fiber variation of salps occurs depends on the capacities of reducing the fecundity of heterozygotes by the chromosomal rearrangments in the stasipatric model of speciation and on the population structure of the species in the clinal parapatric model. If population densities on both sides of the "step" in the cline become high enough to enlarge geneflow between the populations, the cline might become more smooth.

CONCLUDING REMARKS

In salps this speciation perhaps should be called Sisyphean speciation. Because of their sexual/asexual breeding cycle salps are able to multiply very fast (cf. Heron, 1972). Variation in population densities on one or both sides of the step in the cline depending on, for instance, seasonal influences may result in a steeper step one season and a smoother step in another season, thus resulting in a never ending process of speciation, as long as environmental conditions do not change drastically. If conditions do change, resulting in a reduced geneflow for a longer period, then, due to clinal variation, speciation will occur in a relative short period compared to more homogenous species.

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FACTORS AFFECTING THE BIOGEOGRAPHY OF MID TO LOW LATITUDE EUTHECOSOMATOUS PTEROPODS

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INTRODUCTION

Two of the questions asked by biogeographers are: "What are the main patterns of species distribution and abundance?" and "What maintains the shape of these patterns?" (McGowan, 1971). To answer these questions we usually use geographical distributions which represent a composite of data from many years and different sampling schemes. The quantitative interpretation of these distributions can be difficult due to many sources of variation including both natural and sampling variation. In addition, oblique net tows are most often used because many more of them exist in collections than depth-specific samples so they yield wider geographical coverage. The broad features of geographical distributions can certainly be discerned in this way, but the quantitative aspects (i.e. where are the regions of high and low abundance) are most likely to be obscured. These quantitative aspects, however, are most likely to give us insight beyond simple correlations into those features of the environment which have a causative effect.

MATERIALS AND METHODS

This paper examines data on euthecosomatous pteropods collected with a 1m^2 MOCNESS (Wiebe et al., 1976) over depth intervals of 100 or 150m to depths of 850m or 1000m and over intervals of 10-25m to depths of 200m. Samples were collected in different environments: the Slope Water Region off the East Coast of the United States, Gulf Stream Cold-Core Rings, Gulf Stream Warm Core Rings, the Gulf Stream itself, the Sargasso Sea and both warm and cold core "rings" in the northwestern Gulf of Mexico (Fig. 1, Table I). In all cases in situ temperature and in most cases salinity were monitored as samples were collected. The mesh size (0.333mm) was constant for all tows. Deep tows extended well below the vertical range of all common species. In addition to these samples, all available pertinent literature was examined to supplement findings (Table II).

For this group of zooplankton, the factor which most often makes quantitative comparison to other studies impossible is differences in mesh size.

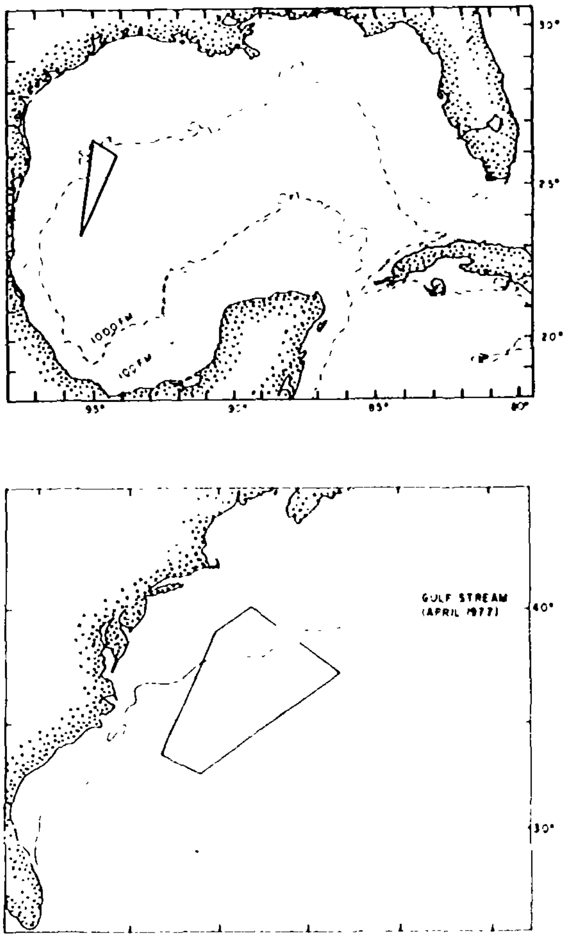


Fig. 1 The sampling areas in the northwest Gulf of Mexico and in the northwest Atlantic Ocean.

Table I Number of MOCNESS tows (8 samples per tow) by environment used in the data base.

Environments	**0 to < 300m**		**0 to >700m**	
	Day	**Night**	**Day**	**Night**
Slope Water Region	2	2	7	6
Gulf Stream Cold-Core Ring Centers	1	3	10	9
Gulf Stream Cold-Core Ring Fringes	-	-	2	5
Gulf Stream Warm Core Rings	-	-	2	2
Sargasso Sea	2	3	8	9
Gulf Stream	-	-	1	-
Gulf of Mexico Cyclonic "Rings"	8	12	1	-
Gulf of Mexico Anticyclonic Rings	7	8	1	-
Totals	20	28	32	31

Work done by Snider (1975) in the Gulf of Mexico showed tremendous differences between the size frequency distributions of *Limacina inflata* and *L. trochiformis* collected in the two sides of a bongo net when different mesh sizes were used (0.183 and 0.505mm) (Figs 2, 3). Other investigators have found similar differences, but this was the first time the samples were collected simultaneously. Although many zooplankton samples used in biogeographic studies probably have been collected for general reference and may, therefore, have depended on available equipment, this quantitative incompatibility underscores the need for some kind of standardization of sampling equipment and techniques in order to derive maximum information from these expensive samples. Sample sizes of about 1000m^3 of water sampled appear to be adequate to collect most species and to give reasonably consistent abundance estimates.

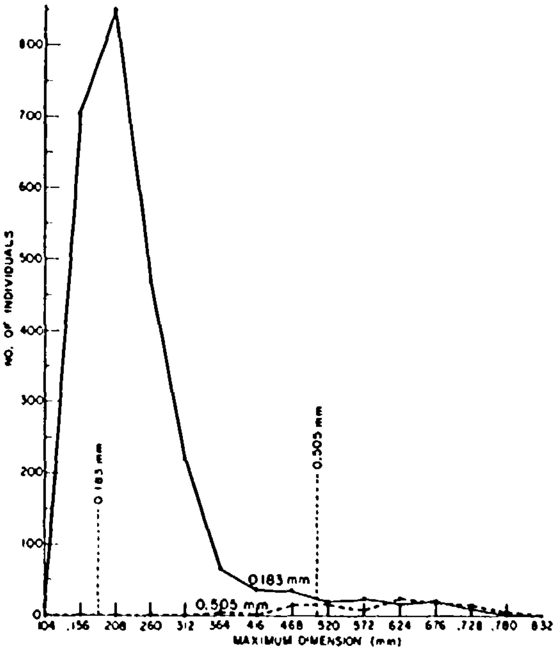


Fig. 2 Size distribution of *Limacina inflata* taken simultaneously with "Bongo" nets of 0.183mm and 0.505mm mesh (0-100m, night) (from Snider, 1975).

Table II Summary of previous distributional pteropod research.

Geographic Area	Depths Sampled (m)	Type of Net	Mesh Size (mm)	Discrete Depth Horizons Sampled?	Investigators
North Pacific	0-140	1 meter	.650	some	McGowan,1960
Western North Atlantic Dow,1953	variable	70cm Discovery net	graded	some	Moore, Owre, Jones &
Bermuda	variable	70cm Discovery net	graded	yes	Wormell, 1962
Western North Atlantic	surface	0.5 meter	.200	no	Chen & Bé, 1964
Northwestern Sargasso Sea	0-150	1 meter	.505	yes	Myers, 1967
Western North Gulf of Mexico	surface	1 meter	.505	no	Vecchione, 1979
	0-100	70cm "bongo"	.333	yes	Snider, 1975
Caribbean	0-4000	75cm Discovery net	graded	yes	Haagensen, 1976
Western South Atlantic	0-137	60cm "bongo"	.333	no	Dadon, 1984
Indian Ocean	0-200	IOS net	.333	no	Sakthivel,1975; 1977
South China Sea	0-200mwo	1 meter	.640	no	Rottman, 1978

RESULTS

Of all species identified, the most abundant and interesting species in most environments was *L. inflata*. This species is a warm water cosmopolite in the Pacific with highest abundance in areas of mixing (McGowan, 1971 see Fig. 1.22). Two different Gulf Stream Cold-Core Rings were sampled twice each during their life histories. The results show that *L. inflata* undergoes fairly rapid increases in water column abundance which correlate with an increase in food supply (Wormuth, 1985). In the absence of measured growth rates, one way to demonstrate the increase is to examine size frequency distributions both inside and outside of the rings sampled. When this was done the corresponding Sargasso Sea populations outside of the Gulf Stream Cold-Core Rings had significantly smaller size frequency distributions. This was interpreted

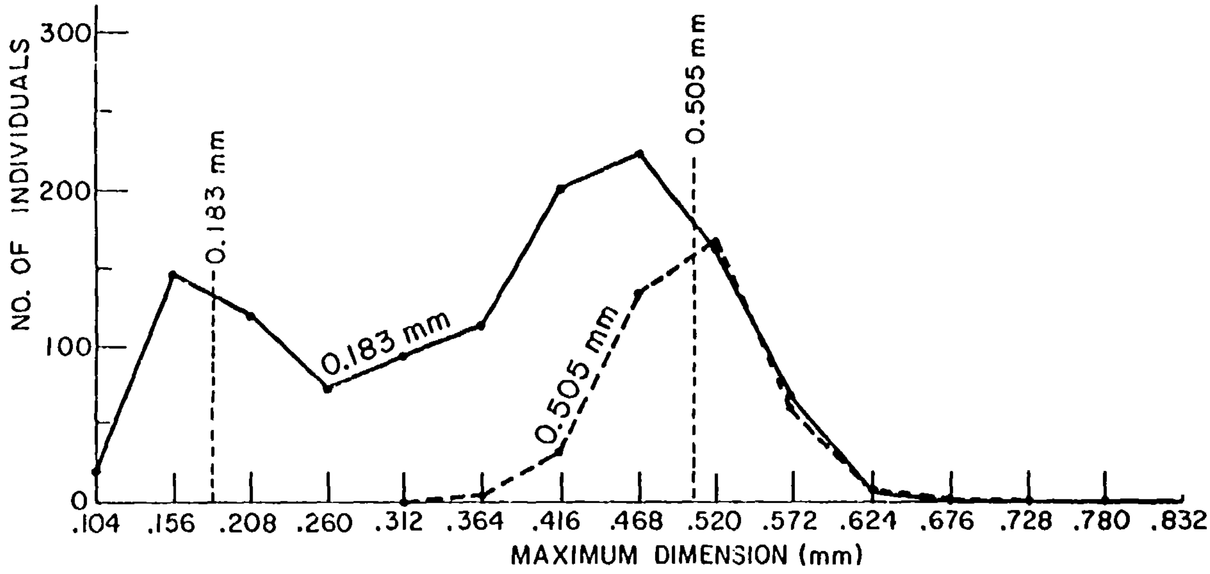


Fig. 3 Size distribution of *Limacina trochiformis* taken simultaneously with "Bongo" nets of 0.183mm and 0.505mm mesh (0-100m, night) (from Snider, 1975).

Table III Rank order of abundance (ROA) of the top 13 taxa by environment.

	ENVIRONMENT (no. of tows)					
TAXA	**SWR (14)**	**GSCCR (20)**	**RF (7)**	**SS (22)**	**GMWCR (7)**	**GMCCR (6)**
Limacina inflata	1.	1.	1.	1.	1.	1.
Limacina trochiformis	2.	7.	8.	9.	11.	2.
Creseis virgula virgula	3.	11.	7.	6.	12.	6.
Styliola subula	4.	4.	4.	3	3.	9.
Clio pyramidata	5.	2.	6.	7.	5.	10.
Limacina retroversa	6.	15.	20.	-	-	-
Limacina bulimoides	7.5	3.	5.	2.	4.	4.
Cavolinia inflexa	7.5	6.	9.	14.	19.	21.
Diacria quadridentata	9.	12.	15.	13.	7.	7.
Limacina lesueuri	10.	5.	3.	5.	2.	3.
Creseis acicula	14.	8.	2.	4.	10.	5.
Clio cuspidata	11.	10.	11.	8.	25.	20.
Cavolinia immatures	18.	9.	10.	16.	6.	7.
Kendall's Corcordance	.30	.46	.76	.77	.56	.81
Probability level	<.01	<.01	<.01	<.01	<.01	<.01

SWR= Slope Water Region; GSCCR= Gulf Stream Cold-Core Rings; RF=Ring Fringe; SS=Sargasso Sea; GMWCR=Gulf of Mexico Warm-Core Rings; GMCCR= Gulf of Mexico Cold-Core Rings.

as indicating a slower growth rate in the Sargasso Sea than in the Gulf Stream Cold-Core Rings (Wormuth, 1985). When the food supply in the rings decreased, so did the water column abundance anomaly of *L. inflata*. This "opportunistic" species can exploit Gulf Stream Cold-Core Rings and is common in the Slope Water Region apparently through seeding from Gulf Stream Warm-Core Rings (Table III). It maintains a population in the Slope Water Region except that it apparently cannot survive the colder winter months (Vecchione, 1979; Myers, 1967). No other species of euthecosomatous pteropods show this type of population dynamics, not even its congeners. *L. inflata* has a unique type of reproductive behaviour in that it broods embryos and early veligers in its mantle cavity, releasing them at 0.066 to 0.068mm (Lalli & Wells, 1973) This behaviour may enhance the survival of young and is not found in its congeners. This could account for its rapid response to rings.

Limacina trochiformis exhibits a different distribution pattern. Although it is a widespread warm water species, it is very low in abundance and quite patchy beyond the influence of boundary currents (McGowan, 1960). It survives in Gulf Stream Cold-Core Rings (while the rings are physically, chemically and biologically more like the parent Slope Water Region than the Sargasso Sea) for a much longer period of time than the cold water species *L. retroversa*, but at much lower abundances - it ranks second in the Slope Water Region and seventh in Gulf Stream Cold-Core Rings based on mean abundance (Table III). In the Gulf of Mexico *L. trochiformis* ranks eleventh in warm core rings originating from the Loop Current and second in cyclonic eddies of unknown origin in the northwestern Gulf of Mexico. When viewed in the context of the overall data base, this high ranking in these cyclonic features is quite unusual. Although there is not an analogues mechanism for the formation of cyclonic features in this area as there is in the Gulf Stream system, the high ranking of *L. trochiformis* and its shelf-type distribution (Vecchione, 1979) suggests a shelf origin for the water. When based on sufficient numbers of samples from various areas, the differences in rank order of species begin to show some explainable patterns.

DISCUSSION

Most vertically migrating species showed little response to differing temperature regimes. Their depth distributions are about the same during the same seasons in the different environments studied (Fig. 4). Nonmigratory species seem to be more temperature-sensitive in that in new Gulf Stream Cold-Core Rings they are very rare or absent. This might be due to the much larger temperature range experience by migrators. More work needs to be done in Gulf Stream Warm-Core Rings to complete this comparison. Most previous studies have stressed the similarities in distributions rather than the dissimilarities, particularly at the edges of species' ranges or of adjacent water types such as Sargasso Sea water and Gulf Stream water or Gulf Stream water and the Slope Water Region. Modern sampling technology allows fairly high sampling resolution and a greater effort should be concentrated in these frontal regions.

Vertically stratified samples should be collected on a scale relevant to the species' biology. Coarse-scale sampling (100m intervals) is useful only for determination of where the organisms are and whether they migrate or not. Samples collected at 10-25m intervals along with physical data and synoptic water samples should help to resolve causative factors from correlative factors. The species studied were always found at shallower depths (14 of 14 tows in the Gulf of Mexico) than the fluorescence maximum (Fig. 5) (when measured) as decribed in other zooplankton studies (Longhurst, 1976; Herman, 1983). A nine-bottle rack of niskin-type bottles is presently being built to be mounted on our MOCNESS. Synoptically-collected water samples could be incubated to examine the relationship between vertical distributions and primary productivity and other aspects of water chemistry. There are also differences in the vertical distributions of size frequency structure of species (Fig. 6) which often are undiscernable by our usual field (mesh size selection previously discussed) and laboratory sampling techniques

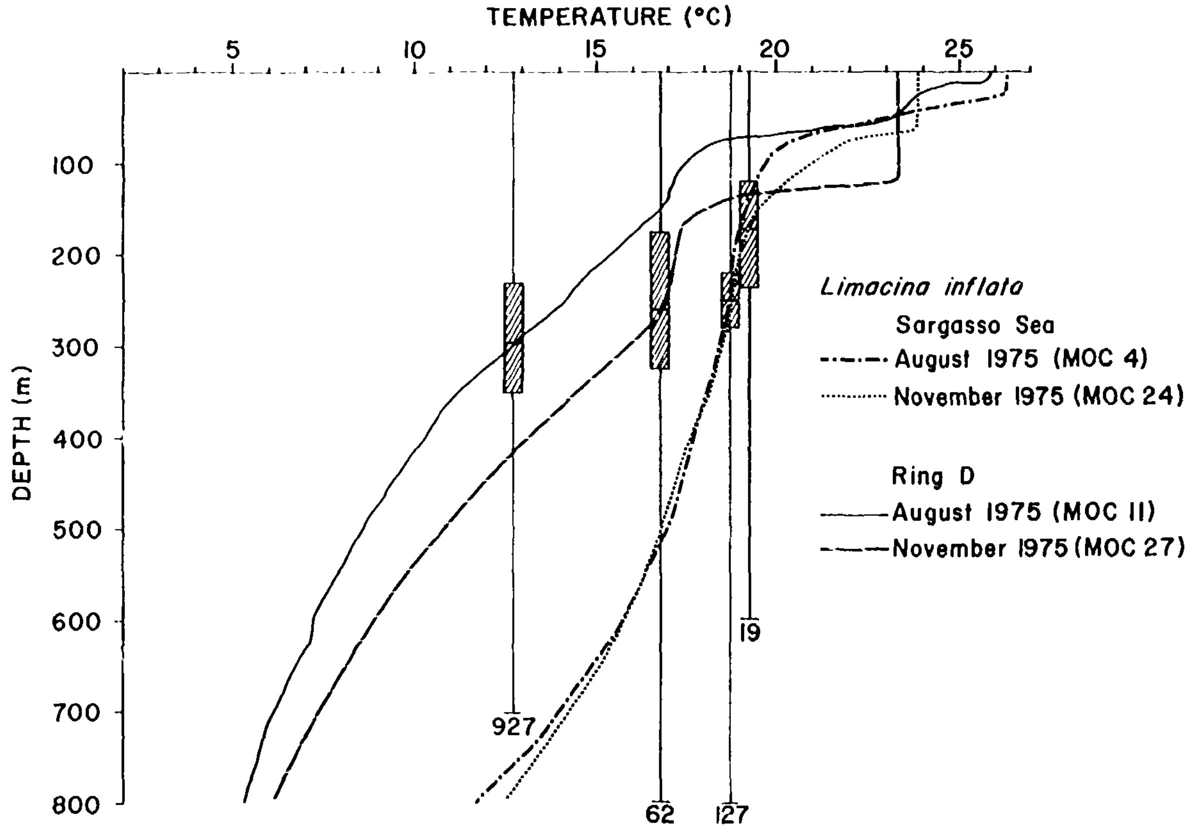
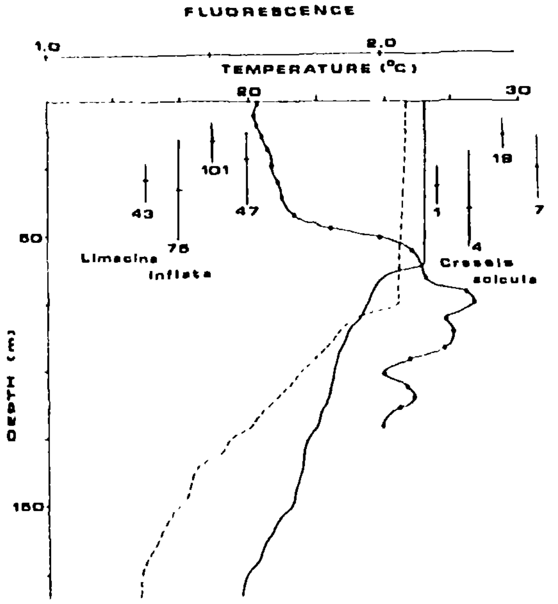


Fig. 4 The daytime depth distribution of *Limacina inflata* in two Gulf Stream cold-core rings and the surrounding Sargasso Sea) and associated temperature profiles. The vertical lines are the total range; the rectangles are the 25th, 50th and 75th percentiles of each population. Numbers below these lines are #/m².



(usually time considerations), but which may provide data useful to biogeographic studies by showing that different growth stages are found in different portions of the water column and are therefore in somewhat different environments.

Tagging rings using satellite-tracked drifters and sampling them at different stages in their life histories appears to have contributed substantial insight into the response of pteropod species to their environment (one resident of the Slope

Fig. 5 The night-time depth distribution of the 25th, 50th and 75th percentiles of a strong migrator (*Limacina inflata*) and a non-migrator (*Creseis acicula*) in the northwest Gulf of Mexico with associated temperature and fluorescense profiles. Numbers below the vertical lines are #/m².

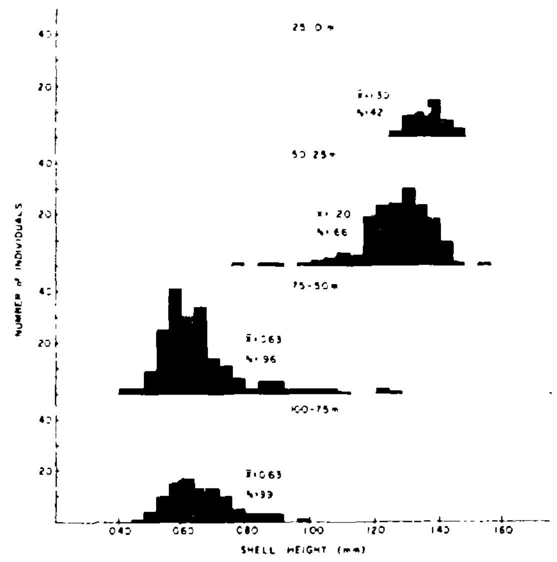


Fig. 6 The size frequency distributions in the upper 100m in the Sargasso Sea in August 1975 for *Limacina bulimoides*.

Water Region water disappears rather rapidly as the environment degrades, one nonresident species of Gulf Stream Cold-Core Rings "invades" rather rapidly and grows quickly and most nonresident species populate Gulf Stream Cold-Core Rings only very slowly as they become more similar to the Sargasso Sea and show no unusual population increases). Although direct experiments have not yet been done, food supply appears to be important (Wormuth, 1985) as one might have predicted. Further, it appears that chlorophyll per se is not the parameter of prime importance. Short horizontal tows at depths of high abundances with synoptic water samples appear to be a logical step to further define environmental parameters associated with both high and low concentrations of individual species.

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PATTERNS OF PHYTOPLANKTON ABUNDANCE AND BIOGEOGRAPHY

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INTRODUCTION

Are the large scale biogeographical distributions of oceanic biology a response to seasonal and spatial patterns of primary production? We ask this question because to us biogeographic boundaries appear as fences behind which taxonomists reconcile differences in species. Could it be that indeed the fences are distributions of food resources and thus dictate biogeographic boundaries? As pointed out by oceanographers Sverdrup and Redfield, geostrophic currents dictate the shape of the density structure. What we term the "degree of baroclinicity" is a global mirror of primary production. The fact is that for at least fifty years we have recognized that climatological factors (i.e., light, wind, temperature) regulate phytoplankton growth. We recognize that seasonality in the primary processes for growth are controlled by the stirring of the upper layers of the oceans and the nutrient-density field which over large scales reflects mass transport of geostrophic currents (Yentsch, 1974; Yentsch, 1982).

Why then are we so hesitant to tie the climatological primary process together with concepts concerning biogeography? One answer might be that we simply do not have enough knowledge of primary productivity over large areas of the world's oceans. The global map of productivity prepared from observations by Koblentz et al., (1969), does not consider seasonal change. With only limited information of time and space change in primary production one is cautious to assign substantive relationships with biogeographic boundaries.

Throwing caution aside, we have selected a region of the Central North Atlantic (Fig. 1) to predict time and space change in the biomass of plankton. The scheme of the prediction (an empirical model) involves using the physiological relationships between photosynthesis and respiration in conjunction with physical features such as the depth of the mixed layer and the nutrient-density field of water masses. This approach attempts to portray in one section of the North Atlantic the time and space changes in phytoplankton biomass. We will compare this portrayal with biogeographic regional boundaries for open ocean myctophids.

SEASONALITY OF "NEW PRODUCTION": THE CONCEPT.

We begin with the premise that stirring of the upper layers by convection and wind is a major mechanism for regulating primary production. The substrates for phytoplankton growth are light and nutrients, and these are regulated

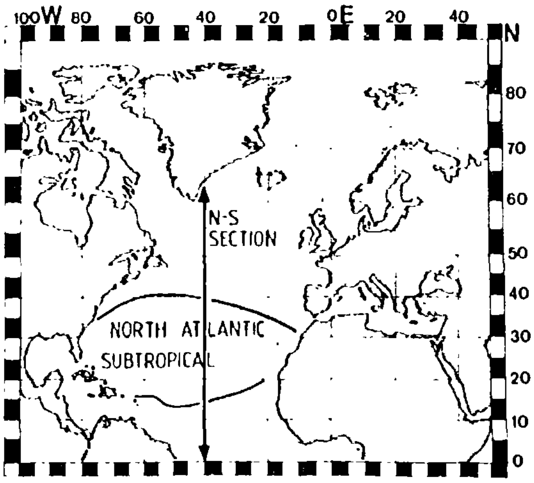

Fig. 1 North sections modeled in this paper. Heavy lines indicate northern and southern boundary for N.Atlantic subtropical populations of myctophids.

climatologically by way of the mixing processes of the upper layers. Thus the physical feature known as the mixed layer is the region of the ocean which couples climatology (light, wind, temperature) with processes which regulate phytoplankton growth.

We argue that seasonality in primary production in time and space is controlled by the movement of the sun from equatorial regions (Fig. 2) to higher latitudes until the summer solstice and then returning to lower latitudes until the winter solstice. This sojourn regulates primary production by deepening the euphotic zone (Z_e) and inducing a shoaling of the mixed layer (Z_m) at high latitudes. The situation reverses as the sun retreats to the winter solstice.

The deepening and shoaling of the mixed layer regulates the mean photon flux density reaching a population of nutrient (N_{Zm}) stirred into the mixed layer and describes potential growth, that is photosynthesis: respiration (P:R).

Thus in concert, these are the factors which influence the seasonality and are the basis of our empirical modeling which follows.

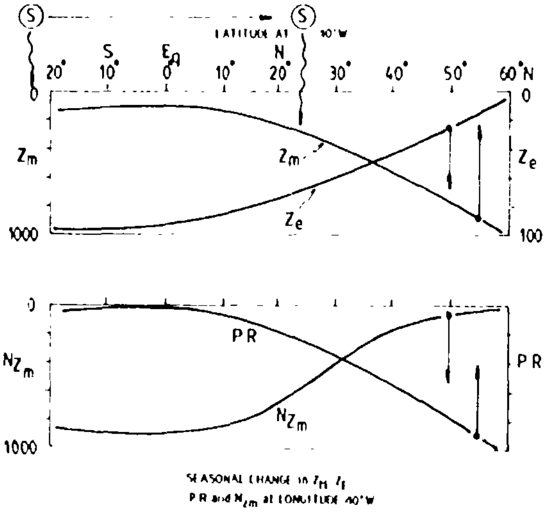

Fig. 2 Hypothetical conception of changes in parameters in section (Fig. 1) due to movement of the sun from Southern to Northern latitudes. Z_m is mixed layer depth, Z_e is euphotic depth. P:R is photosynthetic - respiration ratio, Z_m is the nutrient content of the mixed layer. Positions of the lines represent parameter distribution during the northern winter. The arrows indicate depth change as the sun moves to the north.

SEMI-EMPIRICAL ANALYTICAL MODEL FOR "NEW" PRODUCTION OF PHYTOPLANKTON.

Our modeling efforts require the parameters shown in Table I ((1) P:R relationships and (2) nitrate nitrogen in the mixed layer). These data are used on a monthly basis at each 10° latitude. The P:R in the mixed layer is taken from equations derived empirically by Yentsch (1981)

$$P{:}R\,(1-10) = P{:}R^{*}\,.\,Z_e/Z_m \qquad (1)$$

when (P:R)* is the optimum ratio (10) at light saturation. A P:R=1.0 indicates no net growth. The euphotic depth is calculated by

$$Z_e = \mathrm{Ln}\ I_0 - \mathrm{Ln}\ I_e/K_t \qquad (2)$$

and the amount of nitrate in the mixed layer is

$$N_{Zm}\,(\mu M/M^2) = {}_0\!\int^{Zm} NO_3\text{-}N\,.\,dZ \qquad (3)$$

where, NO_3 - N = μM/kg.

The estimate of production of phytoplankton nitrogen is the product of equtations 1 and 3, where P:R is normalized from 0 (no growth) to 10 (ca. maximum optimal growth). The product reflects the amount of phytoplankton nitrogen in the euphotic layer. Daily production estimates were obtained by dividing the monthly figures by 30.

P:R RELATIONSHIPS IN THE MIXED LAYER

Over the north to south section the mixed layer depth ranges between 30 and 900m (Fig. 3). The deepest layers in this section are confined to latitudes higher than 30°N, and the extremes in depth occur at latitudes higher than 40°. At all latitudes the deepest layers are during winter and spring months (Feb., March, April) and occur at 60°N.

A general rule of thumb is that no phytoplankton growth can occur if the mixed layer exceeds the euphotic depth by five times (Gran & Braruud (1935). The euphotic depth (Fig. 3) ranges between 74 and 40m. With deeper mixed layer depths and shallow euphotic zones at high latitudes during winter months, it is apparent that populations at latitudes higher than 40°N are severely light limited a major portion of the year. This can be demonstrated by the P:R relationships

Table I Parameters for each latitude.

Symbol	**Parameter**	**Units**
I_e	**Incident Solar Radiation**[1]	$cal\ cm^{-2}\ d^{-1}$
Z_m	**Mixed Layer Depth**[2]	**Meters**
Z_e	**Euphotic Depth** [3]	**Meters**
P:R	**Ratio of Photosynthesis to Respiration** [4]	1 - 10
N_{Zm}	**Nitrate Nitrogen in Mixed Layer**[5]	$\mu M/M^2$

[1] Kimball's Tables (1928)

[2] Robinson, Bauer & Schroeder Atlas (1979)

[3] $\ln I_0$ - Lu I_e/K_t where I_e is the minimum photosynthetic radiant energy 1.3 cal cm $^{-2}$ d^{-1}(see Jenkin, 1937).

[4] Empirically derived (Yentsch, 1981).

[5] $N_{Zm} = \int_0^{Zm} NO_3\text{-}N \bullet dz$ (Yentsch, 1981). NO_3-N (µM/Kg) taken from GEOSECS Atlas (1981).

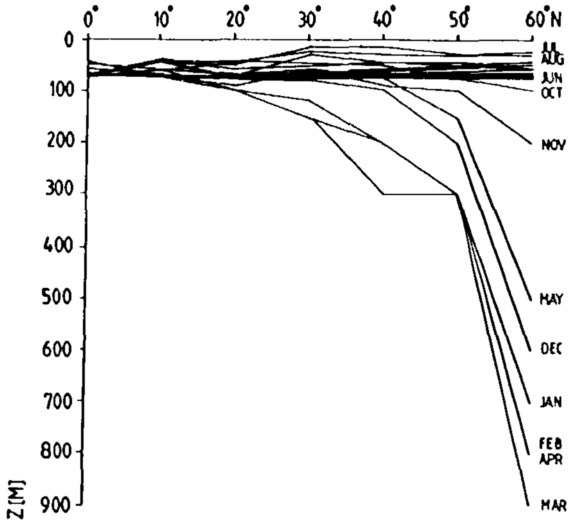

Fig. 3 Seasonal changes in the depth of the mixed layer (Z_m) during winter-spring.

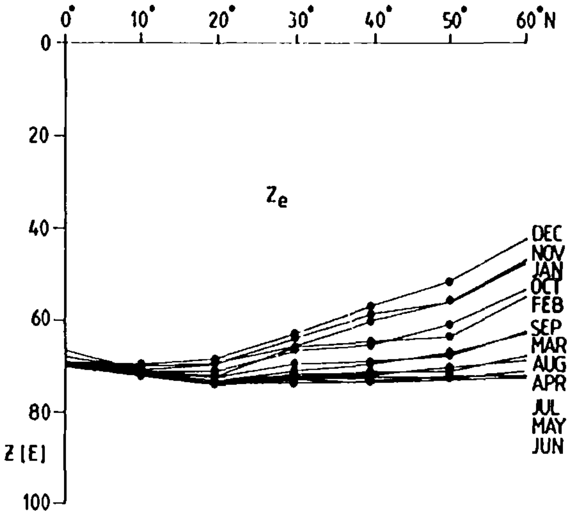

Fig. 4 Changes in euphotic depth (Z_e).

shown as an example in figure 5. During March, light limitation (low P:R) is most severe because solar radiation is relatively low and mixing depth near its maximum. It should be noted however from this figure, that the effects of light limitation are estimated to be observed at all latitudes greater than 10°N with the most severe effects north of 40°.

NITRATE-NITROGEN IN THE MIXED LAYER

We must now demonstrate that changes in mixing depth control the nitrate content in surface layers, but first let us consider the distribution of nitrate. Figure 6 shows the vertical distrib-

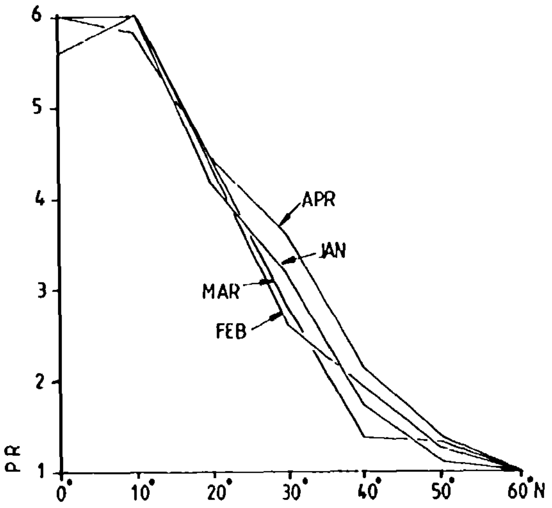

Fig. 5 Seasonal change in the ratio of photosynthesis to respiration (P:R).

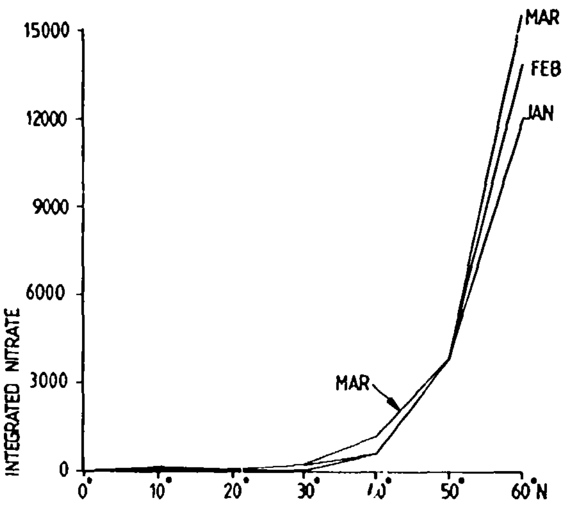

Fig. 7 The amount of nitrate (μM/M^2) introduced to the mixed layer, January through March.

ution of nitrate-nitrogen observed in the GEOSECS transect at these latitudes. The baroclinic effects of the geostrophic currents are apparent at latitudes 40°N (Gulf Stream System) and 10°N (Equatorial system). These baroclinic features are important since it is apparent that as mixed layer depths change it will stir different amounts of nitrate into the upper layers at high latitudes and input large quantities of nitrate into surface layers(Fig. 7). We can speculate that if the mixed layer from the equator to 20°N deepened to 400m, surface waters would be as rich in nitrate as the latitudes north of 40°.

SEASONAL CHANGE IN PHYTOPLANKTON ABUNDANCE AS A FUNCTION OF LATITUDE

Figures 8, 9 and 10 show seasonal trends in phytoplankton biomass at different latitudes. The

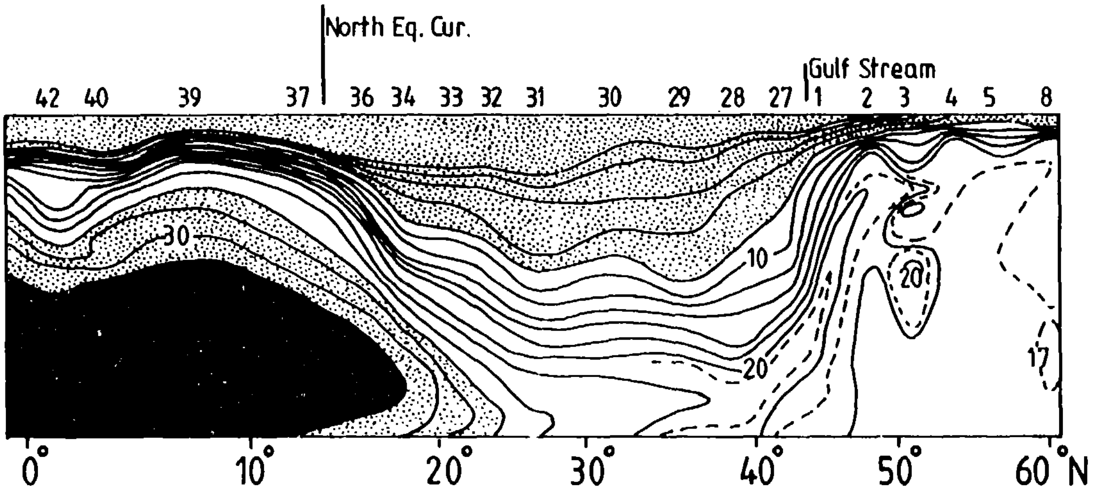

Fig. 6 Distribution of nitrate-nitrogen (μM/kg) from north to south at longitude 40°W.

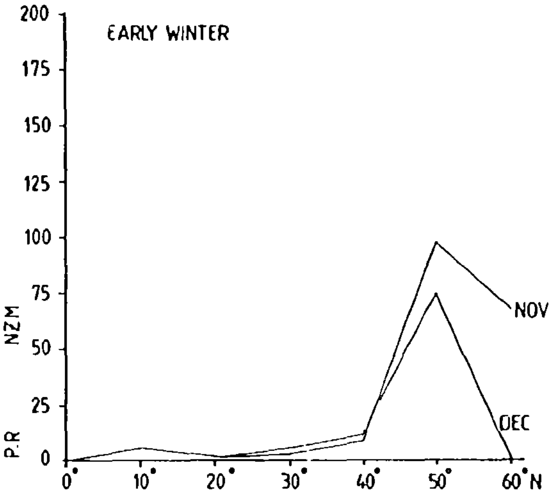

Fig. 8 Seasonal change in phytoplankton nitrogen (P:R x N_{Zm}) in early winter.

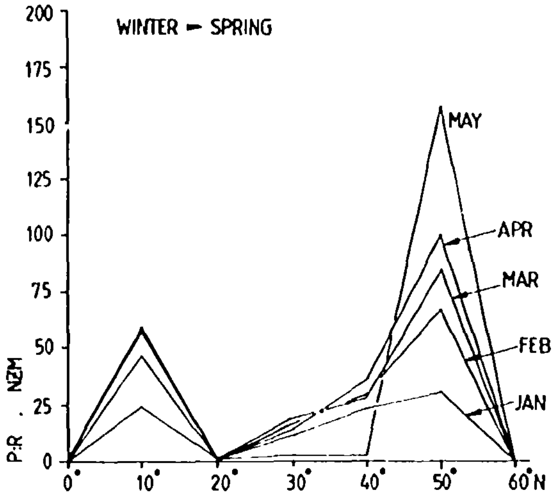

Fig. 9 Seasonal change in phytoplankton nitrogen (P:R x N_{Zm}) between winter and spring.

values (P:R . N_{Zm}) are the product of equations 1 and 3. This product is an estimate of phytoplankton nitrogen biomass in the euphotic zone. If one assumes a 1:1 relationship between nitrate and chlorophyll, the values shown represent euphotic chlorophyll, i.e., the amount in mgs/M^2.

Examination of the trends for all seasons shows two regions of high biomass. The highest is at latitudes greater than 40°N. The next is centered at 10° north of the equator. Lowest estimates are between latitudes 20°-40°N. The period of winter to spring, i.e. January through May, reflected highest stocks at all latitudes. Lowest stocks occur during early winter (November and December). Summer through autumn the section is augmented in phytoplankton stocks at latitudes 50° and 60°N.

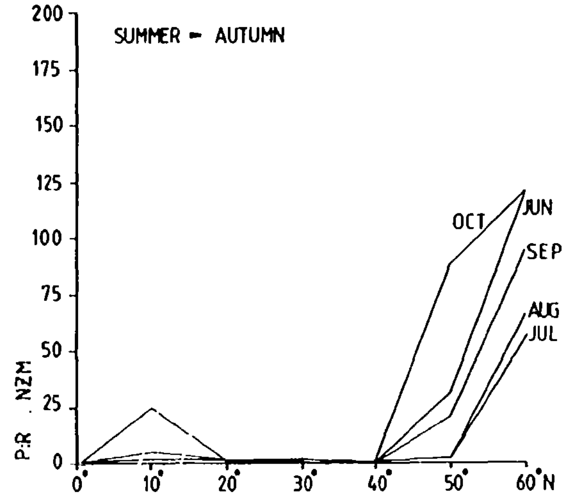

Fig. 10 Seasonal change in phytoplankton nitrogen (P:R x N_{Zm}) between autumn and summer.

These trends in phytoplankton reflect the background of so-called baroclinic patterns of nitrate distribution shown in figure 6. In essence, they reflect the amounts of nitrate entrained by vertical mixing. The high biomass at high latitudes is because the penetrative mixing has greatly enriched the euphotic layers with nitrate. Low stocks of phytoplankton are conversely the result of a shallow mixed layer and/or a deep nutricline. The most important feature in the southern region of this section is the influence of the north equatorial current. The baroclinic features, associated with this current, allow nitrate in the shallower layers to be reached by penetrative mixing rather than in latitudes immediately surrounding them.

THE RELATIONSHIP BETWEEN PHYTOPLANKTON STOCKS AND NORTHERN AND SOUTHERN MYCTOPHID BOUNDARIES

In the Northern Atlantic subtropical region the southern boundaries are the north equatorial current, and the northern boundary is the Gulf Stream. Biogeographers, such as Richard Backus and his colleagues, are aware of the water mass differences between the North Atlantic biogeographic regions. We believe our analysis has demonstrated that the regions could be delineated on the basis of productivity alone. The northern regional boundary coincides with the north limit of the Sargasso Sea and a major change in phytoplankton abundance. The southern limits coincide with the edge of the north equatorial current and also the beginning of a region of increasing phytoplankton abundance. Thus the myctophid populations in the center of the North Atlantic subtropical region are bounded by two geostrophic fences which form the central gyre of the Sargasso Sea. Myctophids housed within this gyre must adapt to the relatively low steady-state production which is known to characterize this region. However, fishes residing at the boundaries of these regions, live in much more productive waters. In these waters, the production of phytoplankton comes in the form of strong seasonal pulses. We can ask whether this region achieves the greatest myctophid abundance? Is it more preferable to reside in the north central Sargasso Sea or in the boundary regions? Scanning the monographs (Nafpaktitis et al., 1977), the distribution of abundance of myctophids appears to show greatest abundance around the northern boundary at approximately 40°N. Some abundance occurs at the southern boundary and in some cases species show no geographic preference for any particular part of the region. The strong relationship to northern boundaries and abundance suggests some unique relationship in temperature and food abundance. It can be postulated that this ideal environment for growth and abundance of these fishes occurs in frontal gradients. This is certainly not a novel suggestion, as many researchers have noted the distributions of an abundance of fishes concentrated in frontal regions.

We believe that the novel information uncovered by our modeling is the apparent geographic stability of the regions of relatively high and low phytoplankton abundance. The fact that while these regions are variable seasonally, they are on the average the sites for high food production over this section. The high production of these regions is maintained by the geostrophic currents and the baroclinicity imparted on the water mass by this flow. This means that as long as these currents continue to flow in these locations, these regions will continue to occupy their relative status as regions of high productivity throughout this region of the oceans. This leads us to conclude that the density nutrient relationships must be fundamental biogeographic relationships of natural oceanic populations. We have observed good relationships between the abundance of tuna assessed by conventional fishing techniques, and distributions of chlorophyll and primary production (Yentsch, 1973). Further, the distributions of species of ocean myctophids falls in the same category, indicating that myctophid abundance is correlated with primary production, which in this case is augmented by the effects of ocean currents. That the stability of these regions should be tested by satellite images which clearly show that the major frontal regions, such as the Gulf Stream system, can be monitored from space and evaluated in terms of position over large areas of the oceans in time.

SUMMARY

A semi-empirical model of new production predicts two major phytoplankton fronts at latitude 10° and 40°N. These correspond to the northern and southern limits of myctophid populations in the biogeographic region of the subtropical North Atlantic Ocean. The persistence of these fronts is due to baroclinic effects of the Gulf Stream in the North and the North Equatorial Current in the South. It is believed that density-nutrient relationships imparted by the movement of ocean currents must be fundamental to the biogeographic relationships of oceanic populations.

ACKNOWLEDGEMENT

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SUMMARY REPORT AND RECOMMENDATIONS

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INTRODUCTION

It is perceived that pelagic biogeography had somehow not shared in the renaissance of interest that had occurred in the last decade for shallow-water and terrestrial systems. Yet study of the open ocean, the largest environment on earth, still relatively unaffected by human activity, offers uniquely-interesting opportunities for studies of evolution, separation and maintenance of distribution patterns of species and of biotas.

The organizers of the International Conference on Pelagic Biogeography attempted to bring together active open-ocean researchers embracing the broadest possible diversity of groups and approaches to discuss the outstanding questions of open-ocean biogeography, where we are, where we ought to be going. The conference programme was designed around nine topic areas, covered in turn by symposium sessions of presented papers and workshop discussion sections.

TOPIC I. WHAT IS UNIQUE ABOUT PELAGIC BIOGEOGRAPHY?

Unique features of open-ocean biogeography center around the vastness, the connectedness and the three-dimensionality of the open sea. There are few geographic barriers and ecotones are often very broad. The recognized faunal regions are the largest on the planet. Open ocean biogeographic studies are typically done at the specific and infraspecific levels as taxa of higher rank (genus and higher) are typically cosmopolitan (or nearly so) within the warmwater ocean. In the open sea -at our current state of knowledge- the concepts of "faunal region" or "community" or "ecosystem" verge on being interchangeable- their boundaries are mapped by recurrent distributional studies.

The very nature of oceans, their vastness and three-dimensional aspect impose considerable constraints upon the methods by which we attempt to develop a coherent understanding of the mechanisms involved in determining and maintaining pattern in biogeographic systems. Repetative sampling over diverse spatial and tenporal scales is neccessary with the difficulties compounded by the need to use different sampling techniques for different organisms. Manipulative experimentation is usually not possible. Fundamental to biogeography is good taxonomy and good taxonomy depends upon the collection of geographically adequate samples, and specimens in good condition. All too often such collections are lacking, due either to inadequate sampling or to the use of inappropriate methods of collection and preservation.

Expatriation is known to occur, what is not known is its prevalence and its significance in the origin and maintenance of biogeographic patterns. Ontogenetic vertical links and their significance have been largely ignored.

TOPIC II. CONGRUENCY OF EPI-, MESO-, AND BATHYPELAGIC PATTERNS

Concordance in distribution among open ocean species of different taxonomic and trophic groups occurs. It is the basis for widely accepted maps of oceanic species assemblages, faunal regions and ecosystems. However, the data that serve as the basis for postulated concordance in distribution patterns have been derived from a multitude of disparate sources and are often reported in ways not directly or easily comparable.

Maps must be constructed using a uniform style and format, with the same agreed-upon standards for inclusion of positive and negative data. The biggest problems involve techniques and scales of sampling that differ by size and nature (e.g. the problem of the "gelatinous" organisms, see Harbison, this volume). Interpretation of historical antecedents of current patterns will involve paleontologic study of historical patterns of organismal distribution and the history of distribution of environmental parameters. Also important to interpretation of the origins of patterns will be meaningful estimates of phylogenetic interrelationships. It seems clear that studies on closely-related species pairs may contribute to our knowledge of the nature and origin of biogeographic boundaries.

TOPIC III. POPULATIONS, PATCHES OR CLUSTERS: THEIR ROLE IN PELAGIC BIOGEOGRAPHY

Genetic populations are considered to consist of groups of organisms within which gene flow is relatively unrestricted. Ecological populations are groups of organisms with similar demographic, morphological and/or behavioural characteristics.

It has not been shown whether different ecological populations (mesopelagic fish, salps, decapods) are in fact different genetically. This might have important biogeographic consequences in terms of divergence and speciation.

It would be of value to determine if centers of abundance are the same (spatially and/or temporally) as centers of populations in either the genetic or ecological sense (cf. Merrett; de Visser; Domanski, all in this volume). Knowledge of this would be presumably be important to the understanding of boundaries. Open-ocean biogeographic maps are essentially boundary plots, typically based on presence/absence data (or, for some groups, charts of relative abundance), no open-ocean species can be mapped at the population level. Genetic studies seem prerequisite to aquisition of such ability.

The concept of communities is based on the co-occurrence of species, the inherent assumption is one of co-adaptation. The coadaptation of species in communities may be expressed most clearly in trophic relationships.

Throughout this session a recurrent theme involved sampling difficulties. In particular the following areas need attention.

There is a need to look at living, in addition to preserved organisms to gain insight into morphological, ecological and behavioral characters useful for systematic and biogeographic understanding. Especially important is the observation of organisms in situ to establish behavioural traits relevant to trophic interactions. This is vital to enhancement of our understanding of community structure as determined by coactive effects and biological accomodation.

Difficulties in sampling large and small organisms on the same scales are evident but must be adressed by improvements of sampling tecniques.

There is a great need to develop new instruments and techniques to address relevant questions in population structure, genetics, scales of distribution and so forth.

TOPIC IV. VARIATION AND THE SPECIES CONCEPT IN OPEN-OCEAN PLANKTON AND NEKTON

It was strongly felt that progress in open-ocean work will neccessitate a greater infusion of modern systematic theory, particularly in available approaches to the estimation of phylogeny.

There have been very few attempts for oceanic organisms to utilize cladistic or numerical or other modern methods, singly or in combination, to produce results based on the greatest possible fraction of the available data. There appears to be no fundamental difference in our concept of what constitutes a species between oceanic vs terrestrial systems. Clear definition of the species concept is essential to open-ocean work because it is at the species level that open-ocean biogeographic work is done.

Recognition of species or of genetically distinct entities in the ocean may be retarded by the tendency to regard the oceans as an environment with weak or non-existent barriers to gene flow, when in fact we know next to nothing about gene flow in open ocean systems.

Contributing as well is the fact that there have been very few studies of variation within broadly distributed species. Such studies of population structure within broadly distributed species will contribute much to our understanding of both what constitutes an open-ocean species and of the reality of biogeographic provinces and boundaries as defined by congruent distribution patterns. Taxonomic results will likely lie on a continuum between recognition of polytypic species (Johnson, this volume) to the identification of distinct new forms (Gibbs, this volume).

Allozyme and other genetic studies have shown that the potential for genetic differentiation is present and operating in the deep sea and that genetic differences occur over short distances. In areas a few hundred square kilometers, distinct populations of some organisms have been recognized.

The biological mechanisms leading to and maintaining reproductive isolation in open-ocean organisms are virtually unknown because (in part) of the great difficulties involved in working with living forms. Greatly needed are additional biochemical, behavioural and physiological studies, breeding experiments, and life history information.

Differences in generation time may lead to a vastly different interpretation of distribution as a function of spatial and temporal scales.

At all times reciprocal study of the interaction between organisms and their environment are needed in behavioural and distributional explanation.

TOPIC V. VICARIANCE BIOGEOGRAPHY

Communities and the ecological relationships defining them also have histories which might be elucidated partially by the fossil record where it possible, for example, to perceive dominance. A potential major contribution of systematics, namely knowledge of phylogenetic relationships, has direct relevance to historical questions.

An important problem is that our present estimate of taxonomic differentiation may in fact constitute significant underestimation for some taxa. Resolution will require additional study and advances in concept and technology.

Questions of short- versus long-term processes were discussed with the novel idea that dispersal may in some respects represent the long-term and vicariance the short-term process.

A number of modes of vicariance were discussed, e.g. orogeny of land barriers, oxygen minima, gacial cycles in the Mediterranean.

A central question involves how to study "hydrotectonic" events. There was some agreement that the water mass system is, perhaps analogously, a tectonic system of its own, directly affecting pelagic biotic distribution to a much greater extent than more remote plate tectonics processes and events.

Identified sources of clarification include syntheses of knowledge of modern organismal and water mass distribution patterns with historical information/inference based on phylogenetic and paleontologic studies.

TOPIC VI. VERTICAL DISTRIBUTION: STUDY AND IMPLICATION

Vertical segregation of close-related species can result in allopatric ranges at a single geographic position.

There is a relationship between the scales of horizontal distribution patterns with depth. The scales increase with increasing depth, but this relationship may break down in the benthopelagic.

Sampling must adequately cover the full vertical range, otherwise vertical vs. horizontal distribution patterns cannot be described.

It is important to emphazise the effect of sampling scale. If sampling is conducted within a limited area, the vertical zonation pattern appears to be clearly-related to depth-correlated parameters. At larger sampling scales, the influence of gross circulation patterns, as indicated by the water mass structure of the water column, becomes more apparent.

Differential ontogenetic vertical migration patterns appear to be strongly correlated with available food supply. Such differences are often magnified in horizontal distribution patterns. Larval and adult ranges are often different with the larvae more stenotypic. Such patterns appear to be part of the linkages between overall productivity, particle-size spectra and ecological adaptations with depth.

One question adressed was the reality of speciation within oxygen minimum regions. Evidence was discussed for the existence of specialized endemics with highly-restricted horizontal ranges within regions defined by a well-developed oxygen minimum. Widespread distribution of sapropels in both on- and off-shore deposits implies that in the past, deep oceanic waters were frequently stagnant for long periods of time. Such conditions may have greatly modified horizontal distribution patterns.

Since any organisms which fail to synchronize their cycle with the circulation characteristics would get lost from the system, this could conceivably result in sufficient separation of synchronized and asynchronized populations to result in differentiation. However, it is unlikely that all such vertical migrations are or can be tuned to smaller-scale circulation cells because of the unpredictable variability of the cells.

TOPIC VII. THE ROLE OF LIFE-HISTORY STRATEGIES

Studies of life histories of pelagic species must include field observations of natural populations to define both the spatial and temporal distribution of a species. This may be enhanced through laboratory experimentation and the development of mathematical models.

Evolutionary life-history theory may provide models to explain the adaptive significance of life-history patterns.

Needed are models involving both ecological and evolutionary time. Especially interesting might be models of life history strategies in "cold vs. warm" ecosystem areas, elucidating benefits of alternation of generations, relationship between life history parameters and abundance and size of distributional range, or net production as a balance between fecundity and dilution.

The study of biogeography should not only document present geographic distribution patterns, whether of species or faunas, but also lead to an understanding about how such patterns have come about. Without the study of life histories such an understanding is not possible. Vital is the recognition that not all life history stages are congruent in distribution and that organisms in different stages of their life history will have different requirements. Unknown or uninterpreted differences in morphology at different stages, not to mention differences in physiology, behaviour, length of time at different stages, periodicity of reproduction, dispersal mechanisms, all may add to act or interact to affect spatial and temporal distribution patterns.

It was also noted strongly that plankton samples exist whose usefulness has not fully been exploited and in some studies could allow avoidance of repetition of expensive field programs.

TOPIC VIII. BOUNDARIES AND TRANSITION ZONES

As used in the following, "transition zone" is taken to denote an area superimposed between two regions defined in terms of their physics, i.e. subtropical or subarctic gyre, or between species assemblages recognized on congruency within and species distinction between such areas. It is important to note that most such zones in the literature correspond to physical transitions or frontal zones, e.g. between gyres or between gyres and circumpolar current regions. The biological conception and identification of such zones is badly blurred by the non-synoptic data sets typifying oceanic biological sampling and established collection data basis.

In regard to species these regions tend to contain representatives from the regions bounding it and its own set of endemics as well.

It is clear that the boundaries between regions will depend on the criteria used in their definition, varying for example as to whether a percentile curve, physical indicator or maximal distribution contour is chosen. It was proposed that to establish the "range" of an organism, its reproductive range is the "true" one.

The nature of rings with their identifiable, ling-lived character, and their close analogy to other frontal features makes them a natural site for process-oriented studies of biogeographical boundaries.

The strong link in the biological nature of frontal boundaries is perhaps strongly tied to the phytoplankton standing crop and its species composition on either side of a front. A fuller understanding of the special advective/diffusive regime associated with frontal boundaries and its effect on various types of organisms represents an essential goal for ecological understanding of open-ocean biogeography.

TOPIC IX. THE ROLE OF REGIONAL AND TEMPORAL VARIABILITY IN PRIMARY AND SECONDARY PRODUCTIVITY

Major geographic boundaries are formed by processes associated with, 1) the general circulation of the oceans; and 2) seasonal effects which influence vertical mixing at upper layers. Major distribution patterns mirror major current patterns. Current mark areas of rapid changes in primary productivity.

Large incremental bursts of production characteristic of high latitudes favour a pattern of energy flow that is different from some low latitude regions where the rate of primary production approaches steady state. It seems not unlikely that the main determinant of distribution patterns is food supply, tempered by seasonality.

This working group proposed that the marine science community should attempt to test this hypothesis.

Priority should be given to expanding our presently limited knowledge of variation in primary production levels and such potentially ecosystem-defining parameters as phytoplankton particle size spectra across regions and boundaries.

The group unanimously agreed that a program of research of this sort would involve synergistic efforts of both pelagic biogeographers and modern marine ecologists.

GENERAL CONCLUSIONS

(1) Pelagic biogeography is the study of the distribution of organisms in the largest environment available to life on earth, the open ocean. Its study involves not only the pelagic realm but connections with adjacent systems. The open ocean is continuous with coastal systems at its boundary and any understanding of either ultimately depends upon study of both. The open sea is linked with the atmosphere via air/sea interactions, with organisms serving as an index to and in certain cases actually influencing interaction. Further, the open ocean is linked with bottom processes; sedimentation, recirculation, and thermal vent processes link bottom and benthos with the pelagic. As a system that is (and has been) essentially physically continuous over time, the open ocean offers unique opportunities for studies ranging from the separation of populations to the development and maintenance of separable communities and ecosystems. Perhaps in no other system is there a better opportunity to employ, and thereby help better define, both ecological and historical approaches to biogeography. Of great importance to this will be enhanced opportunities to relate modern distribution patterns with patterns and changes read from the microfossil record.

2) Understanding modern and past distribution patterns of pelagic organisms and communities requires understanding of and input from virtually all of the open ocean sciences. The very complexity of the subject has contributed to a general lack of rigor in paradigm development, but in a very real sense pelagic biogeography should and can represent a general syntheses of open-ocean biological study. The value of interaction among specialists in diverse areas at the conference became absolutely clear to all. Continued community interaction and periodic meeting was strongly advocated.

3) Whether the study be called taxonomy or systematics, it is clear that the composition of open-ocean faunas and the structure of broadly-distributed species needs intensive additional, practical and theoretical study. Our basic taxonomic knowledge of many oceanic taxa is

woefully incomplete. The conference advocated synoptic (as opposed to merely regional) systematic studies utilizing both traditional and more recently developed approaches, including genetic/biochemical methodologies, cladistic and vicariance biogeographic models, and more emphasis on living organisms, whether in situ or in culture.

4) Sampling remains a continuing most serious problem in open-ocean distributional studies. This follows directly from the unique expense of the pelagic environment. It relates as well to short-term instabilities of that environment that vary by location, time and season, and to different scales of size, mobility and "catchability" of the fauna. Use of varied collecting equipment and methods is required for estimation of any significant fraction of the community. Synoptic sampling of biotic material and abiotic data are additional requirements. Adequate collecting equipment and preservation techniques are essentially unavailable for some of the very fragile (e.g. gelatinous) but wide-spread and ecologically important groups. Greater effort must be devoted to development of such equipment and techniques. Continued gear development is greatly needed, but equally needed are motivated and rigorous studies of sampling theory and design applicable to open-ocean systems and questions.

5) Pelagic biogeographers are fascinated by boundaries and understandably so, for correlated change in boundary zones offers great possibilities for understanding causation of open-ocean distribution patterns. Studies of congruency of distribution patterns should lead to better understanding of community structure and the reality of coadaptation. It should likewise lead to knowledge of edge effects and differences in dispersion in and near boundary zones. Vertical distribution studies across ecosystem boundaries should reflect life history and trophic adaptation to unique ecosystem properties. One workshop group advocated the hypothesis that close correspondence between major distribution patterns and large-scale current patterns is related to marked change in productivity and productivity-related properties (such as particle size spectra) that occur across major current zones. To test and refine this hypothesis whole ecosystem studies in gyre boundary zones are needed.

6) Additional mapping studies are clearly necessary. Equally necessary is the recognition of the treasure house of recoverable information in existing plankton and fish collections and associated cruise/ capture/ locality information. The conference advocated community-wide effort at "institutionalization" of existing collections through survey and through establishment of disciplinary awareness and standards.

7) Other initiatives/efforts/studies identified by more than one workshop group included:

(a) the great need for additional synoptic study of broadly-distributed oceanic species, are they panmictic or polytypic, what is the nature and source of subdivision, how does subdivision relate to recognized ecosystem boundary zones?;

(b) to really understand distribution patterns in any given group there must be a greatly-expanded emphasis on life-history studies involving field, laboratory and theoretical approaches: this is true for all open-ocean taxa although clearly some taxa are less amenable to such study with currently available methodologies than others; and

(c) the potentially important benthopelagic/ pelagic interaction zone is extremely poorly known and deserves greater attention.

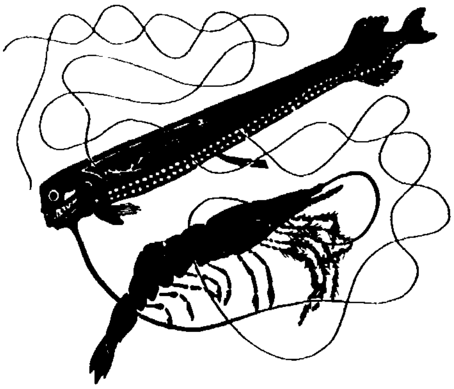
SPECIFIC RECOMMENDATIONS

It is recommended that an ad hoc working group be established to survey, compile and publish a directory of existing plankton collections and their resources.

It is recommended that contact be made with organizers of the World Ocean Circulation Experiment for possible biogeographic-study-related expansion of the biological program.

It is recommended that the conference organizing committee study the appropriateness of seeking establishment of a SCOR working group on pelagic biogeography. The work of this group would involve international collaborative efforts involving each of the general conclusions/recommendations summarized above and such others as the working group or community might generate.

It is recommended that the conference organizing committee remain in contact for the possible establishment of an additional or periodic international meeting of scientists working on the biogeography of pelagic organisms.



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