not always easy to determine whether the higher concentrations or numbers of organisms associated with these flow features result from locally enhanced growth or from concentration by convergent flow. Generally, concentration can only result when there is convergent flow and the organisms have a density different from that of the local fluid.

In recent years, our thinking has generally moved away from the concept that random encounters of patches of predators and prey result in enhanced food web transfers, and toward the concept that persistent or recurring patches (usually associated with certain flow or mixing regimes caused by particular geographical features) have the most potential to affect food web dynamics. The exception to this is the concept that turbulent motions alter the 'contact rate' between individual predator and prey organisms, an area treated in more detail in **Small-scale Physical Processes and Plankton Biology.**

What Remains 'Unknown'?

To what extent has our understanding of the importance of plankton patchiness to food web dynamics been determined by sampling inadequacies? The question can only be answered in the context of how changes in our conceptual understanding have paralleled changes in our sampling capabilities over the last several decades. As sampling capabilities have improved both under laboratory conditions and at sea, we have started to move away from considering patch–patch food web interactions. Increasingly we consider these interactions more in terms of individual predators interacting with individual prey, and determining whether 'contact rate' between predator and prey organisms is regulated mostly by the turbulent flow field or by the actions of individual predators in reponse to their sensing of prey organisms. At sea, even guided by the results of laboratory observations, we can seldom observe individual phytoplankton organisms, so conceptual models have evolved toward consideration of individual predators interacting with patches of prey. Is this the ecologically meaningful view of plankton patchiness? To resolve our conceptual uncertainties we must improve our sampling capabilities such that we can observe individual prey and predator organisms simultaneously over the dimensions of observed patches. The challenge will then be to scale up from the observations of how individual organisms interact with their environment and with other individual organisms to an understanding of how populations of organisms collectively interact with their environment and with other populations of both their predators and their prey.

See also

Bioluminescence. Fish Larvae. Moorings. Plankton. Small-scale Physical Processes and Plankton Biology.

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PELAGIC BIOGEOGRAPHY

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Introduction

The pelagic organisms discussed here inhabit the epipelagic zone where biogeographic distribution of organisms is more complex than in the interior of the oceans.

The epipelagic zone comprises the surface mixed layer, the pycnocline, and several hundred meters into the deeper water masses. In principle, at such depths, water is circulated by the surface currents throughout all the interconnecting basins and marginal seas of the global ocean. Observations of water-mass properties, and of natural passive tracers such as the anomalously low-salinity water that passed around the Subarctic Gyre of the North Atlantic from 1961 to 1981, support this principle.

Though some large fish actively migrate over distances comparable to those of migrating birds, epipelagic plankton and small nekton have insufficient mobility to counter the flow of ocean currents. Apparently, a population of such organisms must go where the water carries it, and this conclusion led early biogeographers to believe that most plankton species must be cosmopolitan.

However, we know that plankton do not behave like passive tracers, although many are widely distributed. There is repetitive pattern in the distribution both of individual species and of associations of species. Only an understanding of the ecology and behavior of individual species will explain how such distributions are maintained, and how regional oceanography determines the characteristic composition of pelagic communities. To understand why individual species are distributed as we observe them to be, it may also be necessary to consider the progressive evolution of ocean basins during geological time. It was this historical aspect of their subject that attracted much of the attention of biogeographers in the past, but pelagic biogeography is now concerned with more than that.

The Pelagic Biota and Their Diversity

The biogeography of the pelagic biota reflects two simple facts. First, although most basic life-forms of metazoa originated in the ocean, relatively few of these invaded the dry land. And, second, the higher plants of the terrestrial flora have no representatives in the ocean, where almost all photosynthesis is performed by single-celled algae and cyanobacteria.

Consequently, the marine fauna is relatively diverse at higher taxonomic levels but has far fewer individual species than the terrestrial fauna. Insect species are more than one thousand times more numerous than copepods because of the (literally) uncounted number of specific insect–plant associations. This illustrates the important generalization that the structural complexity of the terrestrial plants induces a great diversity of ecological niches compared with the poverty of niche-space in the relatively unstructured oceanic ecosystems. The coral reef exception proves the rule.

As in terrestrial ecosystems, diversity in the epipelagic zone of the ocean responds indirectly to latitude. In polar oceans, where there is only a brief, light-limited pulse of primary production near mid-summer, there are fewer species, of fewer sub-phyla or classes, than elsewhere (**Table 1**). In the central oceanic gyres where primary production rate is relatively invariant, both species and higher taxonomic units are the most diverse. Where upwelling occurs seasonally in warm seas, diversity is intermediate. Values for ecological measures of diversity, such as the Shannon–Weaver index, are similarly distributed. These observations conform to the ecological generality that diversity is greater in ecosystems of low than in those of high latitudes.

Such analyses of diversity of the ocean biota are constrained by our uncertainty about the real numbers of marine species, and by the general difficulty of defining the ecologically significant lower taxonomic units of plankton. The 3000-odd species of marine plankton that have been formally described are Linnaean or ‘taxonomic’ species: that is, forms that are distinguishable on the basis of their morphology and to which a binomial (e.g., *Calanus helgolandicus*) is assigned. This classical approach does not describe the reproductively isolated populations that occupy disjunct parts of the total range of many species and that are the significant ecological units.

These expressions of the ‘Rassenkreis’ of Rensch, or of ‘sub-species’ of the ‘biological’ species of Mayr and Julian Huxley, have been satisfactorily investigated in only a few marine organisms, but their existence may be crucial for the persistence of species of plankton and micronekton. Until recenty, our ability to locate such self-sustaining populations was limited to groups whose morphology was amenable to careful numerical analysis – as in the counting and relative spacing of pores in the exoskeleton of some copepods. Fortunately, the sequencing of mitochondrial DNA is now available to discriminate genetically isolated populations with clarity. Even today, because this has been done in very few cases, we remain unsure to what extent Linnaean species of plankton actually have the population structure of biological species. This information will accrue only slowly, but in the interim we may assume that it is the normal case for species that are distributed widely, for reasons we shall now discuss.

Table 1 Percentage composition of zooplankton communities in the Polar, Westerlies, Trades and Coastal biomes, data from 4000 plankton samples, taken randomly over all oceans and sorted into 15 major taxonomic categories

Biomes	*N*	*MEDUS*	*SIPH*	*CHAET*	*POLY*	*CLD*	*OSTR*	*COPEP*	*AMPH*	*MYSI*	*EUPH*	*PENAE*	*PTER*	*APPEN*	*THALI*	*DOLIO*
								Numbers of individuals (%)								
Oceanic																
Polar	7	0.06	*0.15*	*3.88*	0.23	0.00	2.45	*86.32*	0.56	0.00	*0.52*	*0.02*	2.44	3.32	*0.02*	*0.00*
Westerlies	10	1.39	*0.45*	*3.99*	0.54	0.47	3.12	*80.45*	0.81	0.02	*2.77*	*0.33*	1.76	2.79	*0.52*	*0.12*
Trades	13	0.85	*2.61*	*6.38*	0.85	0.14	3.39	*72.31*	0.54	0.15	*3.02*	*1.30*	1.70	3.85	*2.10*	*0.66*
Coastal																
Westerlies	8	0.22	*0.59*	*3.32*	0.39	7.07	0.31	*80.10*	0.78	0.07	*1.02*	*0.27*	1.50	3.51	*0.46*	*0.05*
Trades	12	0.67	*2.11*	*5.83*	0.43	6.46	5.72	*62.95*	0.82	0.02	*1.17*	*3.15*	0.60	5.45	*5.15*	*0.10*
								Carbon equivalent biomass (%)								
Oceanic																
Polar	7	0.23	*0.75*	*8.62*	0.47	0.00	3.05	*67.58*	4.57	0.00	*7.66*	*0.13*	6.73	0.18	*0.03*	0.00
Westerlies	11	3.28	*1.78*	*8.62*	0.47	0.00	3.05	*67.58*	4.57	0.00	*7.66*	*0.13*	6.73	0.18	*0.03*	0.00
Trades	11	1.98	*8.51*	*9.00*	1.10	0.01	2.61	*33.13*	2.58	0.00	*30.21*	*5.02*	2.66	0.10	*2.89*	0.01
Coastal																
Westerlies	11	0.62	*2.66*	*6.51*	0.79	0.78	0.28	*64.66*	5.22	0.00	*11.79*	*1.11*	4.83	0.17	*0.80*	0.00
Trades	11	1.39	*7.88*	*9.81*	0.64	0.48	4.98	*37.51*	4.25	0.00	*10.67*	*15.26*	1.15	0.18	*5.80*	0.00

Italic type emphasizes trends in community composition from high latitudes to low.

N = number of major taxonomic groups (classes, sub-phyla) comprising $>0.5\%$ of individuals or biomass. MEDUS = Medusae, SIPH = Siphonophora, CHAET = Chaetognatha, POLY = Polychaeta, CLD = Cladocera, OSTR = Ostracoda, COPEP = Copepoda, AMPH = Amphipoda, MYSI = Mysidacae, EUPH = Euphausidae, PTER = Pteropoda, APPEN = Appendicularia, THALI = Thaliacae, DOLIO = Doliolida.

Population and Expatriation; the 'Member–Vagrant' Hypothesis

The persistence of local populations may be the mechanism by which bisexual organisms in the plankton maintain a sufficient population density for successful reproduction, as Sinclair has suggested. In the absence of this rich population structure, passive dispersal would result in the encounter rate between individuals becoming too low for sexual reproduction to occur. Organisms with asexual reproduction, such as phytoplankon and perhaps some tunicates, have no such requirement, and consequently algal species are more cosmopolitan than metazoans.

Persistence can be maintained only if each local population reproduces at a rate faster than it loses individuals by passive transport out of its retention (or reproductive) area. Since there are no absolute boundaries in the ocean, all retention areas will be more or less leaky, and individuals will be lost into the general circulation. Consequently, the entire population of any species of plankton comprises both members of the persistent population, and vagrants lost to it. So any sample of plankton will comprise abundant individuals of populations that are characteristic of the region (the dominants) where the sample is taken, together with many less abundant species (the vagrants) transported from other regions, some very distant.

What mechanism ensures persistence of the local self-sustaining stocks, the dominants in plankton samples? It has been widely assumed by biogeographers that the oceanic gyral circulations are sufficiently closed that the conditions discussed above are generally satisfied; certainly, this assumption is valid for some gyral circulations. The central part of the North Atlantic Subtropical Gyre notoriously retains a floating population of macro-algae (*Sargassum muticans*), and the gyre within the semienclosed Norwegian Sea retains a persistent population of *Calanus finmarchicus*.

If we examine more typical situations, we find that simple gyral retention becomes a very incomplete explanation of how populations persist. It is common for disjunct populations to partition a single more-or-less closed gyre, as do species-pairs of North Atlantic copepods. In the cold limb of the Subarctic Gyre, *Calanus glacialis* and *Metridia longa* have their centers of distribution, while the warm limb is the habitat of *C. helgolandicus* and *M. lucens*. Conversely, the related *C. finmarchicus* occurs much more widely throughout the gyre.

How are such patterns maintained? To the extent that flow-fields of ocean currents are laminar, then purposive activity on the part of the organisms must be invoked to explain their persistence. Topex-Poseidon images of the elevation of the sea surface show that flow is nowhere laminar but instead comprises a complex field of cyclonic and anticyclonic eddies having internal flow rates greater than that of the mean current. But because the whole eddy field is itself moving at the mean velocity of the gyral current, the eddies themselves cannot increase overall retention of passively transported biota, except where an individual eddy is captured by topography.

On the other hand, population persistence requiring active behavior on the part of the retained organisms does occur. The seasonal migrations of *Calanus finmarchicus* between the near-surface and 500–1000 m maintain enough individuals in suitable advective trajectories within the subarctic gyre for centers of persistence to be maintained. Populations of *Calanus* spp. and *Calanoides carinatus* of upwelling regions persist by migrating down to the slower and even contrary flow below the newly formed pycnocline at the end of each upwelling event, thus avoiding longshore and offshore transport. At the onset of the next upwelling event, they are carried passively surfaceward and toward the coast. A similar pattern of seasonal vertical migration enables populations of macroplankton in the Southern Ocean to persist within their optimal latitudinal zone.

Most significantly, do the almost ubiquitous diel migrations of many kinds of organisms also serve the same purpose? Planktologists are reluctant to question the current paradigm that diel vertical migration of oceanic zooplankton is primarily a response to predation (as it undoubtedly is in lakes), so this possibility has been largely neglected. But by crossing the shear-zone within the pycnocline and passing 12 h within the slow or even contrary transport of the deeper circulation, many diel migrants must significantly reduce their passive transport within the surface water. This is the concept of Alister Hardy that 'vertical migration sets them striding through the sea with seven-league boots,' although perhaps we should regard vertical migration as a mechanism to increase persistence rather than to enhance dispersion.

Influences of Regional Oceanography on Ecology and Distribution of Organisms

The seasonal cycle of the oceanic phytoplankton is not everywhere the same, each region having a characteristic pattern determined by only a small number of factors, of which the most important are the seasonal sequences (i) of mixing and stabilization of the water column, and (ii) of irradiance in the photic zone. In coastal regions and archipelagos, the effects of tides, topography, and river effluents may force stability, nutrient supply, and irradiance.

The phytoplankton association characteristic of each region differs taxonomically, and with each is associated a characteristic community of zooplankton, both herbivores and predators. It is against this background of regionally characteristic plankton communities or associations that the geographical distribution of individual species must be considered.

Several suggestions have been made to account for the distribution of characteristic plankton communities by reference to regional oceanography. The simplest concept is that each surface water mass is inhabited by a characteristic association of species, some of which may be selected as 'indicators' for the water mass. This model dominated biogeographical research for many decades, but is of limited interest now since it does not address the seasonal ecology of each characteristic association. In recent years this need has been addressed by various proposals for a geographic partition of the epipelagos; for instance, that there are six 'local types' or models of phytoplankton ecology associated with the oceanographic regimes of (i) the sub-tropical gyres, (ii) the eastern boundary currents, (iii) the Southern Ocean, and so on.

A more satisfactory generalization is based simply on Sverdrup's model of the seasonal cycle of phytoplankton. This yields the required general relationship between regional oceanography and plankton ecology. Only if the depth of mixing is shallower than the critical depth, where algal cells are light-limited, can net growth be positive and a bloom occur. This model is applicable to all oceanographic situations and responds to such diverse processes as Ekman pumping, the existence of a low-salinity 'barrier layer' in the thermally uniform surface layer, and tidally forced mixing over continental shelves. Although local forcing of mixed layer depth is usually assumed, the model also accommodates the consequences of geostrophic forcing of mixed layer depth, as occurs widely in the tropical ocean.

The physical processes required for Sverdrup's model are not distributed continuously, but have the discontinuities we observe in regional oceanography, from which has been derived a global partition into 'biogeochemical provinces.' This ecological geography of the epipelagic zone comprises four biomes in the sense of Odum, for whom biomes are the largest ecological units, each having characteristic climax vegetation. These are (i) the Polar biome, where the depth of the surface mixed layer is influenced by the presence of light, low-salinity water derived from ice melt; (ii) the Westerlies biome, where seasonal changes in mixed layer depth are locally forced by winds and irradiance; (iii) the Trades biome, where mixed layer depth may be largely a geostrophic response to distant wind forcing; and (iv) the Coastal biome, where the factors determining mixed layer depth are diverse and are more significant than the effect of latitude itself. Each of the oceanic biomes has a characteristic set of biota and a characteristic seasonal ecological succession. These suggestions recall the earlier scheme of Beklemishev for Polar, Gyral, Transition and Coastal biomes based not on ecology but on recurrent pattern that he noted in the distribution of plankton species.

The boundaries between biomes, located at time-varying discontinuities in regional oceanography, are not symmetric between oceans. The Trades and Westerlies biomes meet at the relatively abrupt transition at the Subtropical Convergences from the strong tropical pycnocline to the weaker subtropical pycnocline. The Polar biome is bounded by the Polar Frontal Zones, where there is an abrupt poleward increase in the stability of the pycnocline. The Coastal biome is bounded by the shelf-break front, generally identifiable above the upper continental slope.

We should not expect conditions within these four biomes to be everywhere uniform, and indeed Platt and Sathyendranath have introduced the concept of dynamic biogeochemical provinces, which are a finer partition but conceptually similar – 'dynamic' because their boundaries are allowed to vary at all temporal and spatial scales, and 'biogeochemical' because each has characteristic environmental and ecological conditions and harbors a characteristic plankton population. Using boundaries defined by frontal regions and other features of regional oceanography, 50-odd biogeochemical provinces (**Figure 1**) have been identified globally, each of which can be individually assigned to one of eight simple models of the seasonal production cycle (**Table 2**). This is not the only possible partition and others will undoubtedly be suggested if the interpretation of satellite imagery, which is the essential and unique tool for such investigations, becomes more widely accepted by biological oceanographers.

Concordance of Biogeographic Patterns

Examination of maps of the global distribution of plankton species (and very many such maps are

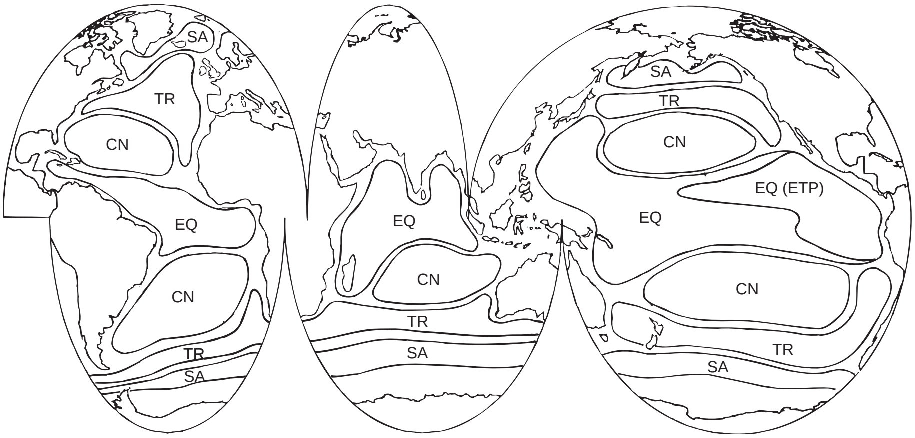

Figure 1 Special biogeography: a generalized arrangement of characteristic boundaries for distributions of oceanic plankton species, excluding Polar forms. Vagrant individuals will occur outside these boundaries, sometimes even abundantly, but are unable to establish presistent populations there. Boundaries for this figure have been redrawn from the suggestions of McGowan and Backus. Sa, Sub (Ant)Aratic; TR, Transitional; CN, Central; EQ, Equatorial; ETP, Eastern Tropical Pacific.

available) led Dunbar to comment that the biogeographic method does not exist, or at least that there are as many methods as there are biogeographers. There are no agreed terminologies for the various types of distribution, or criteria for determining biogeographic boundaries. The problem is in part a consequence of undersampling and in part of uncertainty in the identification of specimens collected at sea, and finally reflects the fact that the motives of biogeographers have been very diverse.

Only in relatively small parts of the ocean has sampling been adequate to draft contoured maps of the seasonal abundance of individual species. Over most of the ocean, we have only limited information on the presence or absence of species and in any event the published maps too often lack conviction because they do not plot 'absence.' However, despite this all-too-frequent lack of rigour, sufficient information is now in hand that we can be confident that the general outlines of pelagic biogeography (in the taxonomic sense) are known. For instance, the distribution maps for many Pacific plankton species published by the Scripps Institution of Oceanography carry conviction that a few consistent and repetitive patterns have been identified, for whose existence logical explanations can be suggested.

Without an extraordinary and unlikely expenditure of ship-time, this situation will not change and we must do the best we can with what we have. But from satellite imagery we can now obtain regional and global maps of the near-surface chlorophyll field, from which we may compute phytoplankton biomass. These images show us for the first time

Table 2 The eight models of seasonal phytoplankton growth that characterize conditions in each of the 57 biogeochemical provinces into which the ocean may be partitioned

Model	
1. Polar biome	Light-constrained summer bloom (6 provinces in cold polar and sub-polar seas)
2. Westerlies biome	Winter-spring bloom terminated by nutrient limitation (15 provinces of the open ocean in mid-latitudes)
3. Westerlies biome	Spring bloom terminated by nutrient limitation (4 oceanic provinces of the North Atlantic and Pacific)
4. Trade Wind biome	Small-amplitude algal growth response to trade wind seasonality (6 provinces of the open tropical oceans)
5. Trades and Coastal biomes	Large-amplitude response to reversal of monsoon winds (Coastal: 4 provinces, Trades: 2 open ocean provinces)
6. Coastal biome	Canonical spring–autumn blooms of mid-latitude continental shelves (parts of those coastal provinces that include mid-latitude continental shelves)
7. Coastal biome	Topographically forced summer production (3 provinces where the continental shelf is unusually wide and level)
8. Coastal biome	Intermittent and seasonal blooms at coastal divergences (6 upwelling provinces, principally in eastern boundary currents)

how one component of the planktonic biota responds to the fine spatial detail of the eddying flowfield of ocean currents.

For just a few cases we have sufficiently detailed grids of samples to infer something of the small-scale distribution of zooplankton species, and these show that this distribution in no way resembles the smooth contoured maps of abundance usually obtained from plankton surveys. One unusually close study shows how the abundance of euphausiids in the California Current matches the details of circulation around interacting eddies, and so conforms to the pattern of the surface chlorophyll field observed in simultaneous satellite images. This demonstration should cause us to ask how best to extrapolate from chlorophyll images to the geographic distribution of other organisms – initially, of course, the herbivores.

All this being said, maps of the surface water masses, of the distribution of individual species, of community diversity, of individual biomes, and of metazoan and algal biomass are nevertheless all remarkably concordant at the large spatial scale. All tend to reflect the zonal distribution of oceanographic properties, most clearly in the Southern Ocean and North Pacific, and less so in the North Atlantic and the monsoon regions of the Indo-West Pacific. Thus, the zonal Polar and Subtropical Convergences are prominent not only in maps of oceanographic properties but also in many distributions of species and biological properties. Similarly, the pattern of zonal currents in the equatorial zone is captured not only in oceanographic maps but also in satellite imagery of chlorophyll and in distributions of individual species of plankton.

Biogeographic analysis at this level of abstraction does not, of course, explain the differential distribution of individual species. Generalization in this special aspect of biogeography depends on the recognition and analysis of repetitive pattern expressed in individual distribution maps, which must reflect not only the circulation and ecology of the present-day ocean but also (as already noted) the geological evolution of the ocean basins.

A distribution pattern that caught the attention of the early biogeographers, and that seemed to falsify the concept that all plankton were cosmopolitan, is of species that seemed to occur in both polar oceans, and only there. But modern surveys and taxonomic analysis have shown that many of these so-called ‘bipolar’ species really have much wider cold-water distributions, by progressive submergence equatorward. Just a few truly bipolar species are presently acknowledged, and the real status of these awaits genotype analysis of the disjunct populations in boreal and austral seas.

Because the Atlantic is clearly more isolated from the Pacific than from the Indian Ocean, systematists (unable clearly to discriminate between taxonomic species and populations of biological species) are more likely to accord specific status to populations divided by the American continent, which reaches very far to the south, than to those with greater possibility of exchange around the southern tip of Africa. Consequently, many taxa widely distributed in the warm regions of the Indo-Pacific appear not to occur in equivalent zones in the Atlantic, being replaced there by a related, but apparently different species.

Those few cases where critical population analysis has been performed show that the real situation may be very complex, as DNA analysis of many disjunct populations of *Cyclothone* demonstrate. The eastern Pacific population of this small pelagic fish has greater genetic affinity with that of the western Atlantic than with the other Pacific populations. Disjunct populations must be relatively stable, since no genetic drift has occurred since an eastern population was divided into Atlantic and Pacific stocks by the closure of the Panamanian isthmus. And it also shows that populations within a single ocean basin are able to retain their genetic isolation without intermingling. Such complexity is perhaps not unusual and may be a typical pattern of pelagic biogeography; many populations of closely related species are likely organized in this way.

We may take the maps of distribution of Pacific plankton drafted at Scripps Institution of Oceanography as the best available representation of how Linnaean species are distributed in an entire ocean basin. The observed distributions of individual species of several phyla may be grouped into six repetitive patterns (or ‘biotic provinces’), each of which in turn can be associated with features of regional oceanography, or with surface water masses. Perhaps the most satisfactory group synthesis is that for euphausiids, because it includes a vertical component, enabling us to compare distributions in the epipelagos with those in the interior of the ocean.

In the open Pacific, three distribution patterns of euphausiids are recognized (**Figure 2**): (i) ‘Central species’ of the subtropical gyres; (ii) ‘Equatorial species’ occupying the zone from 20°N–20°S, extending somewhat into the western boundary current and including a further partition of a triangular eastern equatorial zone); and (iii) ‘Transitional species’ lying along a narrow belt in each hemisphere at about 40° latitude, and extending equatorward somewhat into the eastern boundary currents. These are ideal distributions, as is made clear from the degree of spatial overlap between them, and species substitutions

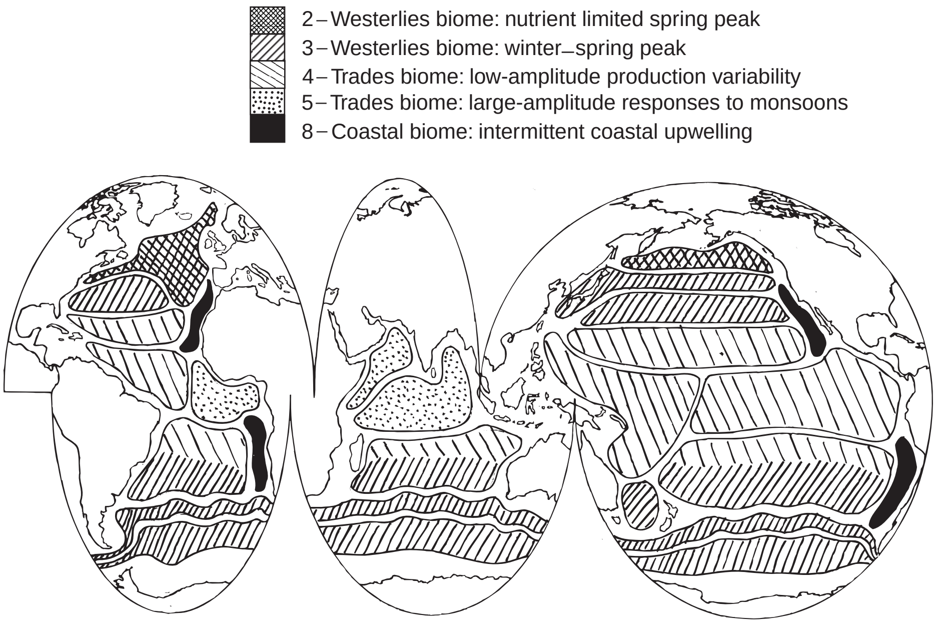

Figure 2 Biogeochemical provinces: a simplified arrangement of the 50-odd Sverdrup provinces into which the ocean may be partitioned (see text), but excluding most of the Coastal biome. The figure also illustrates the distribution of five of the eight models of the seasonal cycle of phytoplankton production, based on the Sverdrup model, which are detailed in **Table 2**.

occur between equivalent zones in the two hemispheres. The Transitional zone is associated with the oceanographic subtropical convergence zone, where eastward transport occurs in a very active eddy-field lying between the subarctic and subtropical gyres. Some species of zooplankton and nekton appear to be endemic to this zone, but phytoplankton blooms are derived opportunistically from algae from both subarctic and subtropical gyres, whichever happens to be have been advected into the Transitional zone when conditions are appropriate for a bloom to occur.

So much for the great reaches of the open Pacific Ocean. Marginally, eight neritic species of euphausiids comprise a ‘Boundary’ group and about the same number comprise a ‘Subpolar’ group, four each in the Subarctic Gyre and the Subantarctic Current. A further set is specific to the Antarctic Current and coastal waters. It is suggested with good reason that species distributions of most groups of planktonic organisms can be accommodated in only about half-a-dozen patterns, together with a residue of more apparently cosmopolitan species. Once again, however, it should be emphasized that it is very probable that modern population analysis will demonstrate genetic differentiation within these apparently cosmopolitan taxa.

These distribution patterns of individual species of plankton and micronekton support – by their overlap, and their open boundaries – the member – vagrant hypothesis, and they also conform very well in their general arrangement, and in some of their actual boundaries, with the arrangement of biomes and smaller ecological or biogeochemical partitions based on regional oceanography and the Sverdrup model.

More remarkably, there is very close concordance between the distributions of individual species of oceanic tuna and the biogeochemical provinces of the Westerlies and Trades biomes, whose distribution is discussed above. This is all the more remarkable considering the ability of these fish to migrate rapidly over great distances. In the eastern tropical Pacific, yellowfin and skipjack are closely constrained within the boundaries of two biogeographic provinces defined by criteria from regional oceanography, while in the North Atlantic, bluefin tuna distribution supports the east–west division of the Subtropical Gyre into two provinces.

From the excellent concordance we can now observe between the distribution patterns of all kinds of pelagic organisms, both with each other and with maps of processes forced by regional oceanography, we may reasonably conclude that, after a difficult start, the way is now clear for biogeography of the pelagic habitat of the open oceans to take its place among the serious disciplines of biological oceanography. Further progress will require work both at the molecular level, in the analysis of genetic isolation of populations, and with satellite-borne sensors to understand better how the single biological variable we can reasonably hope to measure synoptically and globally – the biomass of phytoplankton – is forced by regional oceanographic processes.

See also

Diversity of Marine Species. Large Marine Ecosystems. Ocean Gyre Ecosystems. Polar Ecosystems. Primary Production Processes. Upwelling Ecosystems.

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PELAGIC FISHERIES

See **OPEN OCEAN FISHERIES FOR LARGE PELAGIC SPECIES; SMALL PELAGIC SPECIES FISHERIES**

PELAGIC FISHES

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Introduction

In the economy of the sea pelagic fish play a central part. The simplest food chain comprises phytoplankton, copepods and pelagic fish. They spend their lives in the midwater of coastal seas and oceans. Much of our knowledge about them comes from the fisheries that exploit them, which yield very large catches. The three groups, clupeoids, tunas and mackerels live in all parts of the ocean and many of them migrate across the seas for considerable distances. The clupeoids include such fishes as herring, sardines and sprats which have supported large fisheries since the earliest times. Anchovies are widespread and the Peruvian anchoveta once supported a very large fishery. Herring are caught in the North Atlantic and North Pacific; sardines are taken in the upwelling areas and sprats are mainly caught in the North Sea. Herring can migrate for up to 2000 km each year and their stocks (or populations) have yielded annual catches of as much as one million tonnes, wet weight. They are smallish fish ranging in length from about 12 cm (sprats) to 20 cm (sardines) and 25–30 cm or longer (herring).

The tunas are larger fishes, one or two meters in length and each year they make transoceanic migrations. They include yellowfin, albacore, bigeye and bluefin. Catches amount to about a million tonnes each year and they are taken at many places in the world ocean, but particularly in upwelling areas and at fronts. Mackerels are larger than herring (up to 40 cm in length) and they also migrate across considerable distances. The common mackerel in the North Atlantic and the cosmopolitan Spanish mackerel are typical examples; horse mackerels (in a different suborder) are also widely distributed. The pelagic fish spend their lives in the near-surface layers of the ocean and they swim steadily for long periods. From their central position in the marine ecosystem they control the passage of energy up