The Pelagic Oceanic Assemblages of the Sargasso Sea Around Bermuda

Martin V. Angel

Number 1 Sargasso Sea Alliance Science Report Series

SARGASSO SEA ALLIANCE
GOVERNMENT OF BERMUDA

When referenced this report should be referred to as:

Angel, M.V. 2011. *The Pelagic Ocean Assemblages of the Sargasso Sea Around Bermuda.*
Sargasso Sea Alliance Science Report Series, No 1, 25 pp.
ISBN 978-0-9847520-1-0

The Sargasso Sea Alliance is led by the Bermuda Government and aims to promote international awareness of the importance of the Sargasso Sea and to mobilise support from a wide variety of national and international organisations, governments, donors and users for protection measures for the Sargasso Sea.

Further details:

Dr David Freestone, Executive Director, Sargasso Sea Alliance, Suite 300,
1630 Connecticut Avenue NW, Washington D.C., 20009, USA.
Email: dfreestone@sargassoalliance.org

Kate K. Morrison, Deputy Director, at the same address
Email: kmorrison@sargassoalliance.org

The Secretariat of the Sargasso Sea Alliance is hosted by the Washington D.C. Office of the International Union for the Conservation of Nature (IUCN).

Website is **www.sargassoalliance.org**

This case is being produced with generous support of donors to the Sargasso Sea Alliance: Ricardo Cisneros, Erik H. Gordon, JM Kaplan Fund, Richard Rockefeller, David E. Shaw, and the Waitt Foundation. Additional support provided by: WWF Sweden and the Pew Environment Group.

COVER PHOTO: Porbeagle shark, A. Murch.

ISBN 978-0-9847520-1-0

The Pelagic Oceanic Assemblages of the Sargasso Sea Around Bermuda

Martin V. Angel

Research Fellow
National Oceanography Centre
Southampton, UK

Foreword

BETWEEN 2010 AND 2012 a large number of authors from seven different countries and 26 separate organisations developed a scientific case to establish the global importance of the Sargasso Sea. A summary of this international study was published in 2012 as the "Summary science and Supporting Evidence Case." Nine reasons why the Sargasso Sea is important are identified in the summary. Compiling the science and evidence for this case was a significant undertaking and during that process a number of reports were specially commissioned by the Sargasso Sea Alliance to summarise our knowledge of various aspects of the Sargasso Sea.

This report is one of these commissioned reports. These are now being made available in the Sargasso Sea Alliance Science Series to provide further details of the research and evidence used in the compilation of the summary case. A full list of the reports in this series can be found in the inside back cover of this report. All of them can be downloaded from **www.sargassoalliance.org.**

Professor Howard Roe
Science Advisory Committee Chair
Sargasso Sea Alliance

Professor Dan Laffoley
Science Coordinator
Sargasso Sea Alliance

The Pelagic Oceanic Assemblages of the Sargasso Sea Around Bermuda

The inventory of species inhabiting the interior of the ocean in any region results from the complex interactions of short-term and long-term phenomena. The distributions of the deep pelagic assemblages in the deep ocean are essentially four-dimensional (longitude, latitude, depth and time). There is an inventory of species, which potentially can occur that is the product of evolutionary history and factors controlling the dispersion of the species. So, the species composition observed at any moment is a product of the organisms' interactions both with the physical environment, some aspects of which are constantly being modified over long and short time scales, and the biological interactions within the assemblages (such as competition for resources and predation). The Sargasso Sea provides an environment which is in some ways unique, so that it is inhabited by a heterogeneous mosaic of species assemblages. This mosaic carries the imprint of some unchanging physical properties of water, planetary forces imposed by the Earth's orbit around the sun, the moon's orbit around the Planet and the physical forcing of the Earth's spinning, tectonic events that over geological epochs have determined the physical structure of the ocean basins, and at shorter time scales climatic oscillations, and one-off 'weather' features. Superimposed upon these abiotic influences are biotic factors determined by the day-to-day behaviours and interactions between the constituent species.

Physical properties of water – unchanging abiotic factors

Water is translucent but not transparent. Even the purest water absorbs light and scatters. Consequently there is no detectable daylight at depths below 1000m. In addition the different colours (wave-lengths) of light are absorbed (and scattered) differentially by the water. The red wave lengths are absorbed most quickly, whereas blue-green light penetrates to the greatest depths. At depths below 100m a red object will appear black because there is no red light for it to reflect. Thus the light becomes progressively more monochromatic with depth. At ocean depths below about 1000m, even in the clearest ocean there is no daylight. Thus, the greatest volume of living space in the Sargasso Sea, as in rest of the deep ocean (and the Earth's habitats in general) is dark. There is some light because in dark environments organisms produce their own light (bioluminescence) for various forms of communication.

Another feature of the oceanic water column is that the ambient hydrostatic pressure systematically increases with depth. Some physiological processes are sensitive to pressure, especially those that involve the gaseous phase substances. Thus fishes that use a gas-filled swim bladder to maintain neutral buoyancy or to detect 'sounds' in the water are physically restricted to inhabiting the upper few hundred metres partly because of the escalating physiological costs of maintaining the gas at greater and greater depths, but partly because the buoyancy provided by the gas diminishes.

In situ water temperatures get colder with depth; a result of global climatic processes. The density of seawater is determined by its salt content (salinity) and temperature. When ice forms in polar regions, the water left behind after freezing becomes denser since it is not only very cold (seawater freezes at about -1.9°C) but also saltier, so it sinks. In some polar places, it sinks all the way to the bottom of the ocean, and contributes to the bottom water masses that spread throughout the global ocean (and also oxygenates the deep ocean). So at the greatest depths in the Sargasso Sea water temperatures are 2-3°C, because the cold bottom water spreads northwards from the Southern Ocean across the abyssal plains that lie to the west of the Mid-Atlantic Ridge.

Long-time scale phenomena

a. Tectonic events

The Atlantic is a relatively young ocean compared to the Pacific. The Sargasso Sea began to be formed during the break-up of the supercontinent of Pangea when the American and African plates that carry the continental land masses split apart about 125 million years ago (Parish and Curtis 1982). New ocean crust is formed along the mid-ocean ridges by the ejection of hot molten magma. It continues to shrink as it cools after its formation and slowly spreads away from the mid-ocean ridges. Thus the underlying ocean crust gets deeper towards the ocean margins. However, it also becomes covered with an ever deepening drape of marine sediments in the open ocean and also by terrigenous material close to the continental margins. In the Atlantic the margins are passive; the ocean crust is not being subducted below the continental plates. This means there are no deep ocean trenches in the Sargasso Sea. However, in the neighbouring Caribbean there are some island arcs with volcanic islands, which are fringed by deep trenches. Mean ocean depths in the Sargasso Sea are somewhat shallower (~5500m) than corresponding basins in the Pacific which are >6000m deep. This has an important influence on the character of the deep sea deposits because calcareous skeletons of plankton (such as foraminiferans) that sink to the bottom tend to accumulate in the Sargasso Sea, but dissolve in the deep waters of the Pacific.

The African and American continental plates are continuing to drift apart at a rate of about 1-3cm per year. This has an important connotation for the ecology of the eels. When the eels evolved about 60 million years ago their spawning grounds were quite close to the continental margins. As the Atlantic opened up their migration routes to reach European rivers have progressively become longer. However, the pattern of the ocean currents they exploit for these migrations are determined by the spin of the Earth and so have remained consistent in spite of the extensive climatic fluctuations that occurred during the glacial cycles.

The tectonic event, which has probably had the greatest impact on Sargasso Sea deep oceanic environments occurred some 35 million years ago at the end of the Cretaceous era. The Tasman Seaway to the south of Australia opened up and created an unobstructed pathway for the Circum-Antarctic Current to develop. This had a significant impact on the internal temperatures of the global ocean. Bottom-water temperatures which, at the time, have been estimated to have been about 10°C progressive declined to the present 0-2°C (Shackleton, 1982). The 'ventilation' of the deep ocean with water derived from the surface, substantially increased the concentrations of dissolved oxygen in the deep water.

Currently Central America physically separates the Atlantic from the Pacific, but about 5 million years ago tectonic movements resulted in the Isthmus of Panama being breached opening up a shallow channel between the Pacific and the Caribbean (and hence the Sargasso Sea). Exchange of water through this channel will have mixed the epipelagic faunas of the two oceans, but the deeper living assemblages will have remained segregated. Even within the confines of the Atlantic the deep water assemblages to the east and west of the Mid-Atlantic ridge (>2500m) are almost completely segregated. The barrier is interrupted by two narrow Fracture Zones, one almost on the equator, the other close to 10°S. Flow through these Fracture Zones is predominantly from west to east. So at these great depths, there is greater exchange of water and biological communities coming from the Southern Ocean then from the Eastern Atlantic.

b. Planetary cycles

Another set of forcing processes on ocean processes is provided by the planetary processes resulting from eccentricities in the Earth's orbit often described as the Milankovitch cycles. During the last few million years these cycles are thought to caused the climatic oscillation between the glacial and interglacial eras. These have resulted in rises and falls of sea level of about 100m as the polar ices caps have waxed and waned (note these changes in sea level were probably matched by the impact of the Messiinian salinity crisis resulting from the closure of the Strait of Gibraltar and subsequent drying up of the Mediterranean followed by the catastrophic re-flooding of the Mediterranean during which global sea levels will have fallen by about 70m.) Surface sea water temperatures will have fallen during which the glaciations and risen again during the interglacials. Storminess has also increased during the glaciations. Although these changes in sea-level will not have had a direct impact on oceanic conditions in the Sargasso Sea, the variations in storminess and sea surface temperature will have had an effect. The patterns of ocean circulation, which are largely determined by the Earth's rotation will have been consistent, but both the rates of circulation and the temperature gradients in the upper ocean will have been substantially changed. Similar, but less extreme fluctuations, will also have occurred during the period of climate amelioration that occurred during the 9^{th} – 11^{th} centuries when the Vikings were able to colonise Greenland, and in the mini-Ice Age during the 18^{th} century, which coincided with the first settlement of Bermuda.

c. Shorter time scale events

There are shorter time scale phenomena which will be affecting the Sargasso Sea ecosystem. In the Atlantic the North Atlantic Oscillation (NAO) is a complimentary phenomenon to the North Pacific Oscillation, which is in turn linked to the El Niño/La Niña cycle. The NAO has characteristic periodicities of 8, 24, and 70 years, and in some way these are synchronised with biological oscillations. In a recent study of copepod populations in the upper 200m of the Eastern Atlantic along a transect from 60°N to 63°S Woodd-Walker et al., (2002) observed that the copepod communities are characterised by high, stable taxonomic diversity and a relatively even distribution of genera at latitudes <40° but at latitudes >40° the diversity and evenness are lower and far more variable. More recently Piontkovski and Castellani (2009) have reported that a 10-fold drop in copepod biomass has occurred in the tropical Atlantic (just to the south of the

Sargasso Sea) that is positively related to the NAO-index and phosphate concentrations. They suggest that these changes are linked to a latitudinal widening in the ranges of tropical species and a thinning of the thermocline.

Mesoscale eddies and Gulf Stream Rings are even shorter-term phenomena that have a substantial direct impact on the pelagic communities of the Sargasso Sea. The rings are generated by the spawning of eddies from meanders in the flow of the Gulf Stream northwards along the margin of the east coast of America. The rings that impact on the Sargasso Sea are cold core eddies, which consist of concentric rings of different water masses, together with their original pelagic communities. They have diameters of 100-200km, and when newly spawned the surface sea surface temperature in the core is several degrees cooler that the surround oceanic water and there is a lowering of sea surface, which is 'visible' to satellites fitted with altimeters. Around the circumference of the eddy is a cyclonic band of current that is thrown into a series of meanders. Where the meandering current is turning clockwise there is down-welling, but when it is turning anticlockwise localised upwelling is induced.

These localised patches of upwelling stimulate high productivity, which is further enhanced by the wind/eddy interactions (McGillicuddy et al., 2007). Their impacts are discussed below.

Meddies are also reported to have an impact on the Sargasso Sea. These are deep eddies centred at depths of around 1000m which are generated at the warm saline outflow of water from the Mediterranean that spills through the bottom of the Strait of Gibraltar. Most Meddies move northwards and stay on the eastern side of the Atlantic, but a few move westwards and cross over the Mid-Atlantic Ridge into the Sargasso Sea. They have no surface signature and are difficult to locate and track, and so have not been thoroughly characterised biologically. But they can be expected to be introducing expatriate pelagic species at bathypelagic depths.

The seasonal cycle is a dominant feature of all ocean ecosystems. At latitudes <40° the seasonal cycle is not as strongly expressed as at higher latitudes. The thermocline is a permanent feature so the fluctuations in primary production are less than at latitudes where the upper water column is seasonally turned over. Even so the increases in vertical mixing during the cooler and stormier winter fluctuations and the increases in day length in spring, triggers a surge in primary productivity. This surge is quickly followed by an outburst of breeding by many of the zooplanktonic and mikronektonic species resulting in a pulse of larvae entering the plankton in the epipelagic zone. The seasonal variations and the interannual fluctuations have been monitored in Bermudan waters by BATS a globally unique program that has monitored the fluctuations in time and space of the plankton populations and the water geochemistry in the uppers few hundred metres of the water column. *This unbroken long-term series of observations provides the essential baseline data needed for testing and evaluating models of ocean productivity.*

Vertical structure of pelagic communities

The quantity of living organisms in the water (described as the biomass) is on average highest in the epipelagic zone where primary production is taking place. The biomass decreases exponentially with depth throughout the water column as a result of the decline in available organic matter that can be utilised as food. Virtually all life in the deep ocean away from the continental margins is dependent on organic matter produced in the upper hundred metres or so which sediments down into deep water. Organic materials synthesised near the surface become transferred into deep water by various sedimentary processes, including gravitational sinking and active transport by migrating animals. These processes leach out the mineral nutrients necessary for photosynthesis, so they are continually being transported down into deep water where most are 're-mineralised' through the break-down of the organic material by the action of bacteria. Re-supply of these nutrients back up into the surface layers depends predominantly on the physical processes that mix water from below the thermocline up into the wind-mixed layer. In the Sargasso Sea these mixing processes are limited by the strong stratification of the water column. As a result primary production is low and is dominated by the picoplankton, which are very tiny plant cells <1μm in diameter and are too small to sink under the influence of gravity. So the organic matter they contain together with the associated nutrients is cycled through the so-called *microbial loop*. So, most of this component of the production cycle is not exported into deep water but is recycled within the wind-mixed layer.

Generally sedimentary fluxes diminish with depths as they are intercepted and used as food by the detritivores within the water column and are also degraded by bacterial action. Biomasses of pelagic communities decline by an order of magnitude from the epipelagic to around a depth of 1000m and by a further order of magnitude to depths of 4000m (Angel and Baker, 1982). The availability of resources dwindle with depth and the physiological rates of the inhabitants are lowered to cope with the scarcity of food. Despite this decline in biomass, the species richness of the communities increases down to a maximum at about 1000m depth and thereafter declines very slowly towards the full depth of the ocean. Within

10-100m of the seabed both the biomass and the species richness of the pelagic communities once again increase. This is because the sea floor acts as a sediment trap and enhances the availability of resources. The impact of this increase is transmitted back up into the overlying water within the benthic boundary layer, which is an isothermal and isohaline layer that overlies the sea floor and is kept mixed by the frictional effects of the currents flowing over the bottom. These currents are slow (<10 cms^{-1}) but in events called benthic storms can increase by an order of magnitude. These events occur around the peripheries of mesoscale eddies since they extend all the way to the seabed. These intermittent events can extend the benthic boundary layer up to 1000m into the water column.

The early classical studies of the bathymetrical structure of the pelagic communities revealed a consistent pattern of vertical zonation that is most clearly seen in the tropics and subtropics, and is very evident in the Sargasso Sea. The zones were named as :- the *epipelagic* (surface to ~200m), the *mesopelagic* (200-700m) often subdivided into shallow and deep, the *bathypelagic* 700-2500m), the *abyssopelagic* (2500-6000m), the *hadal* (>6000m) and the *benthopelagic* (the lower 100m or so of the seabed). There is no hadal zone within the Sargasso Sea itself, but there are some deep trenches nearby in the Caribbean. Within each of these zones there are changes in the species composition and shifts in the morphological and physiological adaptations to existence within each zone that are related to the distribution of light and the availability of resources. All life in the deep ocean is supported by the photosynthetic production in the upper sunlit layers, which, in the open ocean, is restricted to the upper ~100m.

The epipelagic zone

The upper wind-mixed layer is occupied by an assemblage of organisms and is described as the epipelagic zone. It is within this shallow sunlit zone that there is bright enough sunlight for the plants (or phytoplankton) to be able to synthesise the building blocks of life–the high energy organic compounds–from the carbon dioxide dissolved in the water using energy from sunlight. This process of photosynthesis is quantified as primary production. The rate of photosynthesis is determined by light intensities and also the quantities of dissolved mineral nutrients that are available (i.e. nitrates and phosphates) and some traces of essential metallic ions such as ferric iron. The wind-mixed layer is usually of uniform temperature (isothermal) and at its base is the thermocline. This is a layer across which the temperature decreases quite sharply and concentrations of the dissolved nutrients increase. Since the density of the seawater increases quite sharply down through the thermocline and the upward mixing of water that is richer in dissolved nutrients from below the thermocline up into the wind-mixed layer inhibited. If such conditions are stable, the water in the wind-mixed layer remains devoid of nutrients and the rate of primary production is kept very low. If the thermocline is shallow enough to be above the depth to which enough light penetrates, some primary production will occur within the thermocline and there is an increase in the abundance of phytoplankton which can be detected by the increase in chlorophyll, this forms a deep chlorophyll maximum. Those regions that are typified by low production rates are described as being oligotrophic. Generally throughout the Sargasso Sea conditions are oligotrophic. Some primary production does occur, mostly by very small phytoplankton cells (picoplankton and nannoplankton). These plants cells are very tiny and less then 1µm in diameter (a micron is a thousandth of a millimetre). They are too small to sink under the influence of gravity so their nutrient content tends to be maintained within the wind-mixed layer and is constantly being re-cycled. These tiny cells are also too small for the majority of filter-feeding plankton to extract from the water, and they are mainly consumed by tiny Protozoa.

Another feature of the Sargasso Sea is that when winds are light and the sea surface is relatively calm, Langmuir circulation cells can be generated. These are counter-rotating cylinders of water a few metres wide. Where these cells converge any materials that are on the surface accumulate in windrows, which are lines of floating debris and weed that lie parallel with the wind's direction. Neuston all accumulates within the windrows. Neuston is the term used for an assortment of planktonic organisms that are linked to the very surface of the ocean. Some neuston have floats (such are the sailor-by-the wind *Vellela*, the Portuguese man-o-war *Physalia*, and molluscs such as *Porpita* and *Glaucus*). Other species have special adaptations to life at the surface and many of these species are blue in colour. Notable amongst these are the pontellid copepods which are deep ultramarine in colour and have compound eyes that are divided into an upper half that appears to be used for seeing above the water and a lower half that sees underwater. Flying fish are essentially large members of the neuston that have become adapted to escape most predators by jumping out of the water and gliding away to safety. However, their escape is not assured because the dolphin fish is able to follow their flight and so chase them under water and capture them when they splash down. A number of other neustonic species escape by taking to the air including species of squid and also pontellid copepods. In the

Sargasso the floating *Sargassum* weed communities, which are retained within the region by the surface circulation add a unique structural component to the neuston that greatly enhances the biodiversity of the region.

There is a seasonal cycle in the composition of the plankton communities inhabiting the epipelagic. Although many of the smaller species have short generation times of a few days or weeks, the zone is invaded usually in early spring when production levels peak, by the larvae and juvenile stages of species whose adults are deeper living and include some benthic species. Many marine species have reproductive 'strategies' of overcoming the extremely high odds against the survival of any of their offspring by mass spawning many hundreds or thousands of eggs. The eggs either float up into the epipelagic or the adults migrate up to spawn there. The hatching larvae have morphologies that are usually totally unlike those of the adults, and most are not supply with enough yolk to survive and grow and so have to feed to get enough food. Initially their survival is enhanced by their small size and transparency. The tiny particles they feed on are more abundant in the epipelagic. The death rates through predation and starvation are almost 100%, and it is only by playing the very long odds by producing so many eggs that survival of enough individuals to maintain the species is assured. As the larvae grow and develop they sink or migrate down into deep water and start the metamorphosis into their adult form. These migrations associate with different stages of the life cycles are described as ontogenetic migrations.

In the Sargasso Sea there is a permanent thermocline and so conditions are generally oligotrophic. However, there are processes which lead to mixing in the surface waters. During the winter air temperatures are lower and the surface of the ocean tends to cool and the depth of the thermocline shoals. Violent storms can then result in some stirring of the wind-mixed layer. Hurricane winds can, even in summer, stir the surface sufficient to replenish the nutrients to some extent in the wind-mixed layer and so result in short-lived bloom of phytoplankton. Stirring also occurs associated with the meanders in the current flows that encircle the mesoscale eddies, and these generate small localised patches of slightly enhanced primary production.

In many areas in the Pacific, primary production is also limited by a lack of dissolved iron in the water, which renders the phytoplankton unable to utilise all the available dissolved nitrate. In the North Atlantic, this is not the case, since enough iron is supplied by wind blown dust that is blown across the Atlantic from the Saharan desert near Lake Chad. Such dust events are intermittent, but mostly occur in the Spring. (**NOTE**: The proposal to counter the increases in carbon dioxide in the atmosphere caused by the burning of fossil fuels and hence ameliorate climate change by fertilising the surface of the ocean with iron to enhance rate of primary production would not be totally ineffective in the Sargasso Sea).

During the day the epipelagic zone is occupied by species that are predominantly either small or transparent, implying that visual predation is a factor that plays a significant role in determining the composition of the assemblages. Since the phytoplankton biomass is dominated by extremely small organisms, the grazers predominantly feed by using mucus webs to trap the tiny cells, and include salps and pteropods. The most abundant group of mesozooplankton is the Copepoda; the copepods dominate the plankton populations throughout the water column. At night the species composition changes considerably with the appearance of many larger species, including fish, decapod crustaceans, euphausiids and large copepods that migrate up from deeper layers. Lights hung over the side of a ship at night attract large numbers of lantern fishes, whose eyes reflect red. They are often being hunted by schools of squid. Flying fish laze at the surface with their fins wide-spread and are sometime attacked by dolphin fish. So where do these new arrivals come from? Or have they merely been hidden from view in some way?

Diel Vertical Migration

The early biologists soon discovered that they caught more plankton and greater variety of species near the surface at night than during the day. There were vehement disputes between the advocates that many of the species were migrating up to the surface from deep water, and those who argued that the apparent migrations were just an artefact resulting from the active organisms being able to see and avoid an approaching sampler during the day. Confirmation that the migrations are real first came from their visualisation by sonar devices. Sound-scatters were shown to be moving up at dusk and migrating down again as dawn approached. Acoustic Doppler Current profilers were later used to generate real-time measurements to the rates of migrations. The onset of the upward migrations tended to be triggered by the rate of decrease in light intensity as the time of sunset approached, but once the migrations started they do not necessarily follow the changes in the light regime. Similarly the migration back down into deep water is triggered by increases in the light intensity as dawn approaches. However, the downward migration is often not as well synchronised as the upward one. The theory that is now generally accepted is that the upward migrations results from the exploitation of the greater availability of resources nearer the surface. The downward migration is to escape the increased exposure to visual predation during daylight. There is a rough relationship between the size of an organism and the depth to which it migrates down at dusk. The results of repeated sampling throughout 48h periods at a range of depths, showed that in early summer at latitudes a little to the north of the latitudes of the Sargasso Sea migrations by the mesozooplankton are restricted to the upper 700m. Migrations by the large micronekton such as decapod crustaceans and some species of lantern fishes (myctophids) extend down to a maximum of 1000m at around 40°N. However, data from a number of stations centred at 30°N 30°W show that some of the decapod crustaceans were migrating down to depths of 1200m and one myctophid fish *Ceratoscopelus warmingeri* was migrating to daytime depths of 1600-1700m, the upward journey and the downward journey each taking about three hours to complete.

The order in which the species arrive at, and depart from the upper layers is related to their daytime depths. The species with shallower daytime depths tend to arrive earlier and depart later than those that occupy deep daytime depths. Some of the migrants are herbivorous, such as euphausiids, so they only feed when they are up near the surface. They migrate down with full stomachs, but when they migrate back up their guts are empty having voided their gut contents at their daytime depths. Thus their migrations are contributing to the removal of organic matter from the upper layers down into the body of the ocean.

Attempts at quantifying the redistribution of biomass in the water column suggested that up to 50% of the total biomass in the upper 1000m may be involved in the migrations. The migrations also have a substantial impact on the fluxes of organic material into the deep ocean with the fluxes being generated by the migrants being nearly 50% of the total being sedimented out in the particle flux.

The mesopelagic zone

The boundary between the epipelagic and the mesopelagic zones is marked by a shift in the species composition by day and an increase in the average size of the mesozooplankton. The zone between 200-400m tends to be dominated by gelatinous organisms such as Siphonophora and Chaetognatha. The fishes within this zone tend to have dark backs and silvery mirrored sides and they have rows of light organs (photophores) arranged along the bellies. This pattern is best exemplified by the hatchet-fishes (*Argyropelecus* spp). This is a form of camouflage. At these depths the light has become sufficiently scattered for the intensity at any angle to the vertical being the same, a mirror hung in the water will be invisible because it will reflect exactly the same light intensity as the background. The only angle at which the fish is then vulnerable is from directly underneath as it will be silhouetted against the brightest source of light coming from the surface. The light organs along their bellies serve to break-up their silhouettes. The decapod crustaceans that inhabit the shallow mesopelagic zone are predominantly half coloured red by a carotenoid pigment and half transparent. In the Sargasso Sea this pattern is exemplified by the two decapods species *Systellapsis debilis* and *Oplophorus spinosus*. This coloration makes them very obvious in daylight, but since at the depth they occupy during the day there is no red light left for the red pigment to reflect so it is functionally black. So once again their coloration, which seems so obvious in daylight, is a form of camouflage.

The zone from 400-700m is the deep mesopelagic, and there is another shift in species composition and an extension in the size ranges of the species composing the assemblage. The general appearance of the fishes changes as those with silvery-mirrored sides are replaced by species that are darker in colour. However, the fish that is by far and away the most abundant fish at these depths in the Sargasso Sea, *Cyclothone braueri*, is semi-transparent but still has light organs arranged along its belly. It is small and is not a strong swimmer and is usually a non-migrant, although it may undertake vertical migration during its spawning season. *Cyclothone* must be a contender for being the most abundant vertebrate on the planet.

There is a comparable change in the colour of the decapod crustacean species, with the appearance of species which are totally red. Some of these *Acanthephyra* and *Sergestes* species regularly migrate right up to the surface at night where they can be caught in neuston nets fished an hour or so after sunset. Other large species that undertake extensive migrations from these depths are *Pyrosoma* spp.; these are very large gelatinous colonial organisms that are basically large tubes (up to 1m in length) and produce a general glow of bioluminescence from their bodies. They are filter feeders. Each component organism of the colony draws in water through its own individual inhalent pore on the outside of the colony, filters it through a sheet of mucus and discharges it into the central cavity and thence out through the colony's communal exhalent orifice. These large organisms can extract the smallest living cells. Despite their apparently simple organisation and lack of obvious motile ability, *Pyrosoma* can migrate up from daytime depths of 500-700m right up into the surface layers at night, and return down again at dawn.

Any species that inhabits the mesopelagic zone either has to be a carnivore preying on other organisms around it or a detritivore intercepting and consuming particles that are sinking down from the surface. They can only be herbivores if they migrate up into the epipelagic zone at night. However, the presence of phytoplankton remains in their stomach contents is not necessarily diagnostic of a herbivore (and hence a vertical migrator). Live phytoplankton cells do get entrapped in marine snow, which are aggregates formed around a core of mucus. These 'snow' aggregates become heavy and start to sink, as they sink they scavenge more and more particles and becoming larger and heavier and so their sinking rates tend to accelerate.

Bathypelagic zone

The top of this zone is the deepest to which detectable daylight penetrates, and then it is only the blue-green wave lengths that have not been absorbed or scattered. In this perpetually dark environment intraspecific communication is either by chemical signals (pheromones) or by light signals using bioluminescent displays. Only a few of the large species, which inhabit the top of this zone by day, migrate up at night. So most are non-migrant and have sharply contrasting appearances to their shallow-living counterparts. At these depths food is consistently in short supply, so the organisms are designed to be as economical as possible. Muscles are less powerful, so swimming speeds are slow. Oxygen consumption rates are reduced. Neutral buoyancy is achieved by low energy physiological mechanisms, so gas bladders in fishes are either filled with lipid or lost altogether and ionic mechanisms are used to keep neutral buoyancy. The density of the bodies of these organisms is reduced by their muscles being more watery and their skeletons being less heavily calcified. Hence the deeper-living species tend to be more fragile and susceptible to damage during sampling. Eyes are either highly modified to detect bioluminescent signals or become non-functional. Prey is detected by sensing their movements, and is often either lured closer or ambushed. Mouths tend to be large enough to swallow other creatures as large as the predator and in the case of fishes are fitted with large teeth designed not for biting but for ensuring that once the prey starts to be engulfed it does not escape.

Reproduction strategies are often bizarre. Many species are hermaphrodite undergoing sex changes as they grow. In some angler fish the males become external parasites on the females. Fewer embryos can afford to be produced, but the risk of predation is much lower, so more energy is invested in each embryo. So eggs tend either to carry copious quantities of yolk or the larvae are brooded by the female rather than broadcast into the water. Below the depth to which vertical migrants penetrate, there are only two possible modes of feeding, predation and detritivory.

Biomass of the pelagic assemblage is generally an order of magnitude lower per unit volume at 1000m depth than at the surface (Angel and Baker, 1982). Sedimentary fluxes from the surface are also an order or so lower than at the base of the thermocline. The finer sedimenting particles which are sinking very slowly have had most of their labile organic content stripped out by bacterial degradation. The larger marine snow aggregates sink much more rapidly and have a much higher organic content, but their residence time in the water column is very much shorter. Flocs generated in the photic zone during the Spring Bloom at temperate latitudes have been shown to sink to abyssal depths at rates of 1000m.day^{-1} and so sediment out in a week or so. These snow particles are aggregates and often contain viable phytoplankton cells. As a result organisms that exploit these aggregates are often found with phytoplankton remains in their guts, although they have never been near the photic zone.

Abyssopelagic Zone

The upper boundary of this zone is not clearly defined, but at around 2500-2700m there is another faunistic change. Decapod crustaceans tend to be replaced by mysids and the biomass of fishes declines quite sharply. There is no obvious environmental interface at these depths that may be the underlying cause for this faunal change, and indeed it may be the result of the interaction between a number of factors. This is a zone that has been very poorly characterised. For example, during a recent Census of Marine Zooplankton program during which deep-living zooplankton was targeted, samples collected in the upper 1000m caught no novel species of halocyprids ostracod but over 10 were collected at depths >2000m, increasing the known inventory of planktonic ostracods in the Sargasso Sea to 150 species (Angel 2010); a remarkable result for this element of the planktonic fauna that has been so extensively studied in the region. The standing crop of biomass continues to decline falling to around 1% that of the wind mixed layer at 4000m.

Benthopelagic zone

This zone is probably coincidental with the benthic boundary layer (BBL), which is the isothermal and isohaline layer that immediately overlies the sea-bed. The BBL is generated by the frictional interaction between seabed and the bottom currents mixing the water in close proximity to the seabed. The thickness of the layer is determined by the current velocities which are generally quite slow, but at times these velocities increase by over an order of magnitude. The influence of mesoscale eddies extends all the way to the seabed and these enhanced current velocities occur around the peripheries of the eddies. The height of the BBL above the bottom may increase to 1000m and sediment and organisms are mixed up into the water column. The influence of the BBL on both biomass and species richness in the water column reverses the general decline with depth. There is a plankton fauna specialised for life in the benthopelagic zone, which remains almost totally unstudied, partly because of the inaccessibility of these great depths and partly because of the technical challenges of towing sampling gear in very close proximity to the bottom. On experimental tow collected at a depth of 4000m within 10m of the sea-bed of NW Africa in 1979, collected 25 novel species of planktonic ostracod (Angel, unpublished data). The other groups were never been examined, but this is an indication that the faunal in this zone is not only rich in species but is probably almost entirely novel. A small insight into this fauna was gained by Deevey (1968) who studied the stomach contents of benthopelagic fishes, and described 6 novel species in a new genus *Bathyconchoecia*. The numbers of species in this genus has now risen to 26, but at least another 30 still await description. In the Sargasso Sea the larger mobile epibenthic fauna that can be sampled by benthic trawls, such as fish and decapods, has received some attention, but the macro- and meso-planktonic benthopelagic fauna remains totally unstudied.

General bathymetric patterns

To illustrate the trends that occur within the water column of the Sargasso Sea **FIGURE 1** shows day (in red) and night (in black) profiles of the parameters of the assemblages of planktonic ostracods at a station near Bermuda sampled in April 1972 (Angel 1979) superimposed on the vertical zonation pattern of the assemblages. The ostracods generally typify these patterns except for their avoidance of the 100m during the day.

The profiles clearly show the results of diel vertical migration with numbers of species and total numbers increasing substantially at night in the upper 100m. The abundance profile shows that most of the migration is occurring in the upper 500m. This is typical of mesoplanktonic groups but similar profiles for micronekton would show the migrations extend up from 700-1000m. The maximum species richness is encountered at and around 1000m and then tails off into deeper water. Population abundances decline (note that these profiles are log transformed and cover two orders of magnitude). The profile is bimodal by day with maxima at 100-200m and 500-700m by day, but unimodal in the upper 100m by night. Below the lower maxima the population declines steadily into deep water, which mirrors the trends in the biomass profiles. The profiles of the diversity indices fluctuate in the upper 200m, but note that the information index (H') and the eveness index (J) continue to increase gradually to the maximum depth sampled.

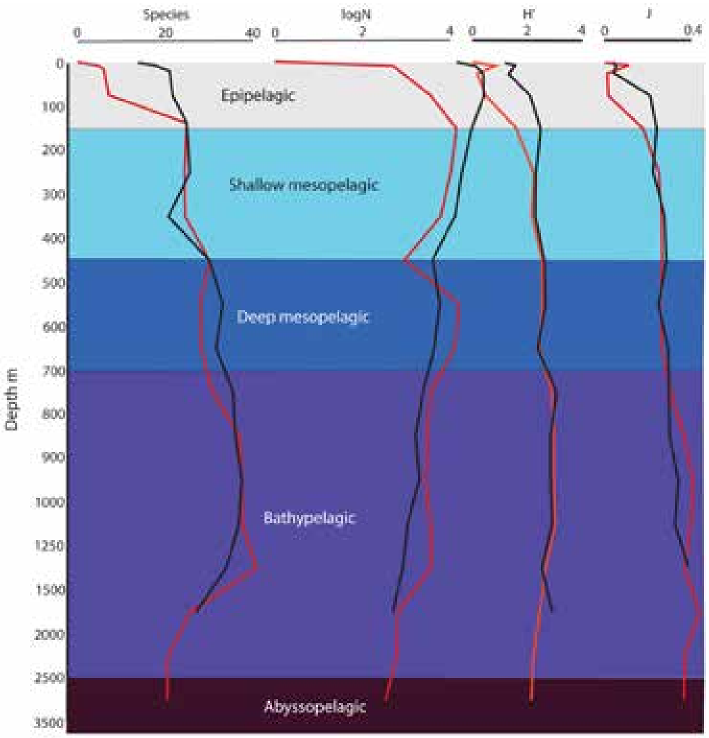


FIGURE 1. Parameters of the planktonic ostracod assemblages at 32°64'W in April 1972. Showing the depth profiles of 1. species richness (numbers of species); 2. Population size (log 10 N per 1000 cubic metres); H' the information index; J the eveness index, and the zonation within the water column.

Some exemplar organisms typifying the zonation within the water column.

1. Epipelagic

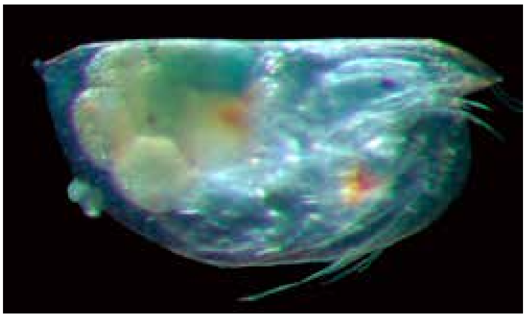


FIGURE 2. A female *Euconchoecia chierchiae* shows many of the typical features of zooplankton of the euphotic zone. It is small (~1.2mm) and is translucent with very little pigmentation *(photo by R. Hopcroft).*

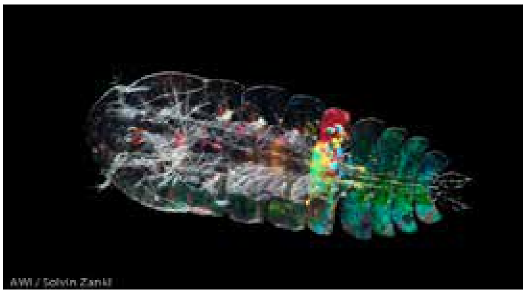


FIGURE 3. A species of the copepod *Sapphirina.* This genus of copepod is very common in the superficial waters of the Saragasso Sea. It is small (~1mm) and almost totally transparent, but contains platelets inside the body that generate flashes of interference colours (c.f. the colour of oil films on water). In flat conditions aggregations of these copepods become visible as they are concentrated in windrows. *(photo by Solvin Zankl/AWI)*

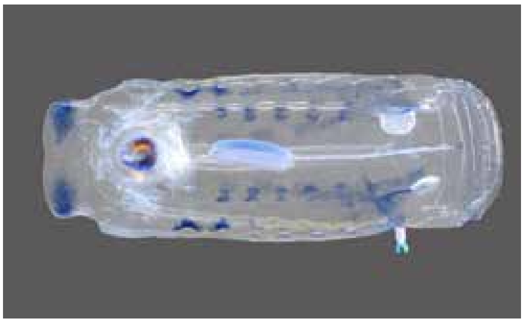


FIGURE 4. A salp *Iasis* sp. showing the blue coloration that is typical of the neustonic species that are associated with the upper few centimetres of the water. The blue colour is often produced by the combination of carotenoid pigments with a protein, and either protects the internal organs of the animal from harmful UV-radiation or camouflages it against the blue of the deep ocean, protecting it from aerial predation by sea-birds. *(photo by Solvin Zankl/AWI)*

FIGURE 5. *Cavolinia longirostris* is a typical species of Pteropoda (sea butterflies). Its molluscan foot is developed into two swimming wings. It traps its food, which includes picoplankton, on sheets of mucus. The shell is constructed of aragonite a mineral form of calcium carbonate that dissolves at depth more readily that calcite, and plays a significant role in exporting carbon dioxide into the deep ocean *(photo by R. Hopcroft).*

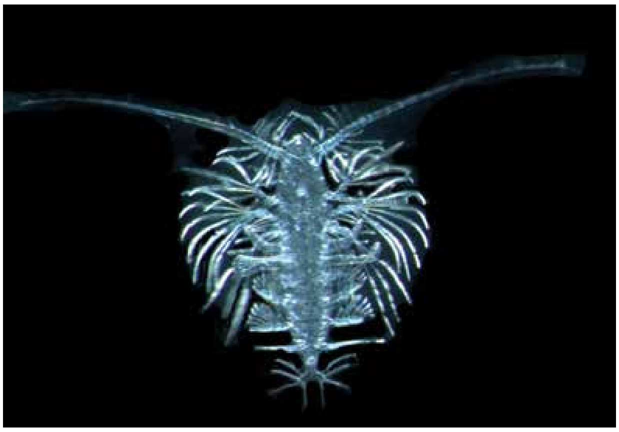


FIGURE 6. A copepod *Haloptilus* that is typical of epipelagic zooplankton, in that it is small (1-2mm) and highly transparent *(photo by Solvin Zankl/AWI)*

FIGURE 7. **A planktonic polychaete worm *Tomopteris*, which is a mini-carnivore in the plankton, but still has to rely on transparency as a means of avoiding predation by predators** *(photo by R. Hopcroft).*

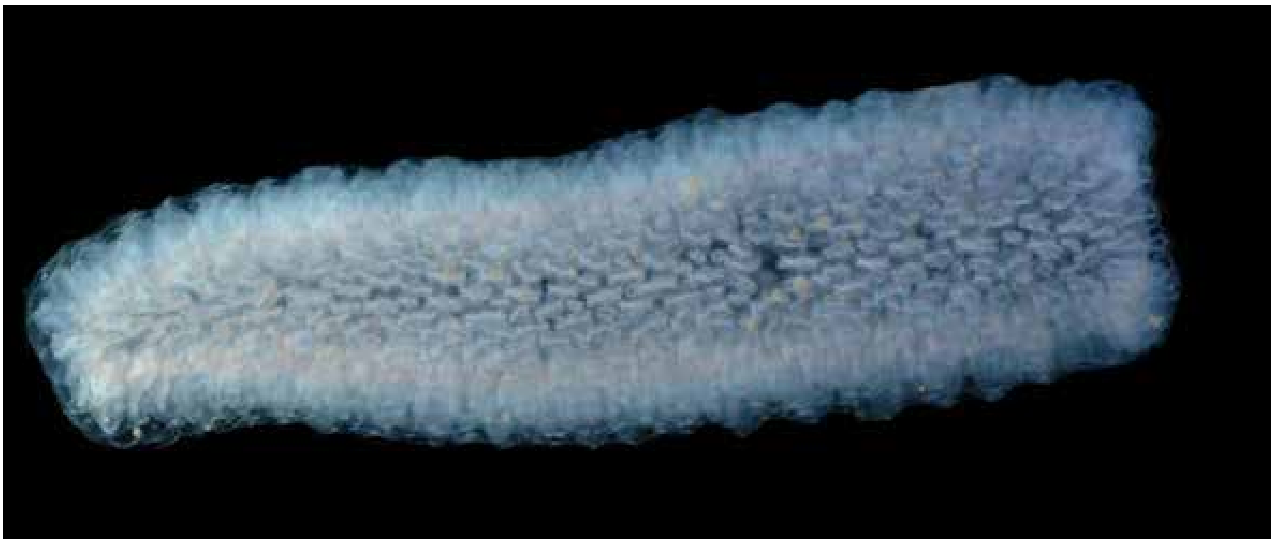


FIGURE 8. ***Pyrosoma*** **are large gelatinous colonial animals that can undertake diel vertical migrations of 500m. They are related to salps and feed by filtering water through mucus sheets moving across the gills of each individual in the colony. This form of filtering feeding enables these large organisms to extract the smallest living cells in suspension in the water. They are also notable because at night they are visible at the surface as their bodies are illuminated with bacterial bioluminescence.** *(photo by Salvin Zankl/AWI).*

FIGURE 9. A shallow mesopelagic ostracod *Conchoecissa imbricata* is an active diel vertical migrant in the Sargasso Sea, that spends the day at 400-500m and swims up into the epipelagic at night. Like most of these migrants when it swims up at dusk its gut is empty, and when it swims down as dawn approaches its gut is full. Thus these migrants are playing a small but significant role in the export of organic matter from the epipelagic zone into deeper water. *(Photo R. Hopcroft).*

FIGURE 10. A siphonophore *Halistemma* is typical of this actively hunting group of gelatinous carnivores. They are extremely fragile and even if they do not disintegrate in a net they fragment when preserved. Hence they have to be studied either by divers or by sampling from submersibles. They are dominant contributors to the biomass of pelagic communities at 200-400m, and probably play a central role in the ecology of the pelagic communities throughout much of the upper 1000m of the water column. Their taxonomy and ecology if probably better known in the Sargasso Sea and the neighbouring seas than anywhere else. There is a gas-filled float at the apex of the stem, then a series of swimming bells which propel the colony through the water, so that they are active hunters. The lower part of the stem is lined with feeding bells and palps which are armed with stinging cells (nematocysts). The stem is very extensible and some of the large individual colonies may extend well over 30m. *(photo by Salvin Zankl/AWI)*.

FIGURE 11. *Argyopelecus sp* a hatchetfish that shows many of the adaptations of mesopelagic fishes. The back is black, but the sides are silvered and acts as mirrors. The belly is lined with elaborate light organs (photophores), which emit light at the right intensity to break-up the silhouette of the fish when viewed from underneath. The eye has a large spherical lens and looks upwards. The mouth is similarly directed upwards and it feeds by spotting plankton swimming in the water immediately above it. This is a fish that is very abundant at depths of 400-600m. *(photo by Solvin Zankl/AWI).*

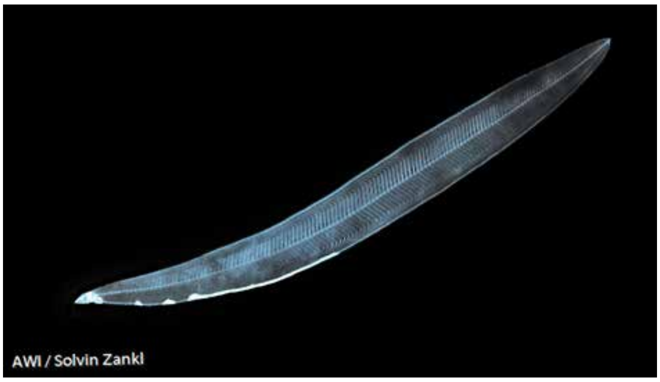


FIGURE 12. Leptocephalus larva of an eel, tend to swim within the thermocline. Note that the body is almost completely composed of muscles. The digestive system is all concentrated in the tiny white dot under the head. These larvae are so transparent that in a sample they are only apparent because their serpentine movements stir the surrounding plankton about *(photo by Solvin Zankl/AWI).*

FIGURE 13. **A *Stomias* species, a typical bathypelagic fish with a long, black, rather snake-like body, a light uncalcified skeleton, small eyes, a big luminescent barbel under its lower jaw with which it entices prey close enough for it to seize it with its long recurved teeth. These fishes can swallow other fishes which are as long as themselves.** *(photo by Solvin Zankl/AWI).*

FIGURE 14. **Whalefish are rare and poorly known fishes that inhabit the abyssopelagic zone. Their eyes at these depths have regressed and most of their perception of the water around them is through chemoreception and movement detection using their elaborate lateral line system.** *(photo by Solvin Zankl/AWI).*

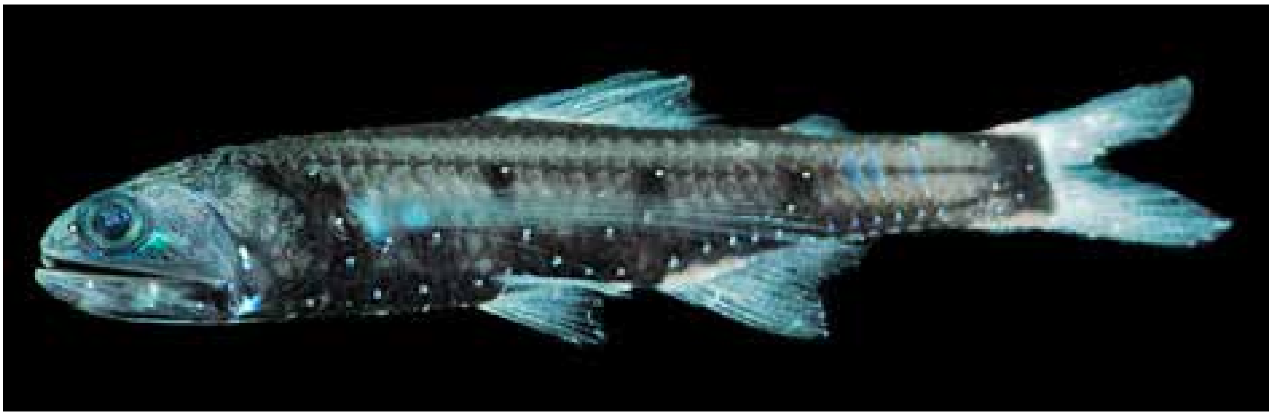


FIGURE 15. **Lantern fish (or myctophids) are a group of pelagic fishes that are extremely important in pelagic assemblages. They are particularly abundant in the mesopelagic zone and many migrate up into the epipelagic at night to feed. Their shoals are responsible for many of the deep-scattering layers that are picked up by echo-sounders. Their eyes reflect red and can often be seen feeding on plankton in the lights from a ship that is hove to at night; where they often attract in schools of squid** *(photo by Solvin Zankl/AWI)*

FIGURE 16. ***Histioteuthis*** **is a common mesopelagic squid in the SargassoSea. Like many fishes the underside of the body is lined with light organs. One very curious characteristic of this squid is that the left eye is substantially bigger than the right. The large left eye has an almost spherical lens and the retina is adapted for the low light conditions in the deep** *(photo by Solvin Zankl/AWI)***,**

Total water column biomass

Angel and Hargreaves (1992) reported that near Bermuda in March 1974, probably just before the main production peak, the total biomass of mesozooplankton taken in a net with a mesh size of 0.32µm in the water column from the surface to a depth of 1000m was 16-20 mls.m^{-2}. These estimates were derived from integrating the data from two sets of 12 depth stratified samples, one collected by day the other by night. The range was in the lower quartile of the range recorded from 22 other stations in the North-east Atlantic, and similar to the values observed elsewhere within the subtropical gyre. The values for the micronekton (sampled with a 8m^2 net with a mesh of 4.5mm) was 5.2-5.6 mls.m^{-2}. In both sets of range the higher value came from a night series, the difference resulting from a combination of net avoidance during the day and vertical migration. These values will vary seasonally and may double when the peak in pelagic biomass that will follow after the peak in primary production (see Deevey 1971, BATS data). Localised peaks will also occur around the fringes of mesoscale eddies where zooplankton production will increase in response to localised increase in primary production as the combined result of growth and immigration. Local increases in micronekton biomass will almost entirely result from immigration, as many species seek out oceanic fronts where the availability of resources is increased; a behaviour that is well known to sports fishermen.

Annual cycle in zooplankton composition

Deevey (1971) gave one of the earliest detailed analyses of the zooplankton cycle in the upper 500m of the water column off Bermuda, using nets with three different mesh sizes. The hauls varied widely between the different samplers, for example a sample collected with the net with 0.366mm mesh caught 30 organisms m^{-3} compared with the net fitted with 0.076mm mesh which caught 615 organisms m^{-3}. She clearly showed the quantities of plankton reached maxima in March/April. Annual and maximum mean numbers of the major groups of zooplankton species are shown in **TABLE 1.**

GROUP	NUMBERS.m^{-3}		% OF SAMPLE	
	RANGE	MEAN	RANGE	MEAN
Copepoda	92-406	195.8	43.6-79.0	69.9
Tunicates	3.6-232.8	27.1	2.3-40.4	7.9
Ostracoda	11.4-36.1	19.5	4.1-11.8	7.4
Chaetognatha	1.3-21.4	8.5	1.0-6.6	3.0
Coelenterata	3.6-18.8	8.7	1.5-4.9	3.1

TABLE 1. Mean density and percentage contribution of the five major groups throughout the year (1961-1962) from Deevey (1971). Note the overwhelming dominance of the copepods that was only diminished in one set of samples when a salp (tunicate) swarm was encountered.

Deevey identified 153 species of copepod belonging to 42 calanoid genera and 20 belonging to other copepod families. The next most abundant group was tunicates, these were predominantly Appendicularia, but also included some doliolids and salps. The swarm encountered was of *Thalia democratica*, which occurred in an estimated concentration of 197 m-^{3}. The occurrence of such swarms of this and other species is not unusual, but tends to be unpredictable.

The occurrence of other groups of plankton was also intermittent and unpredictable. The cladoceran *Evadne spinifera,* the sergestid shrimps *Lucifer faxoni* and *L. typus*, and various pteropods occurred sporadically. Numbers of various types of larvae peaked in association with the spring increase in primary productivity.

Deevey and Brooks (1971) reported on a similar survey, only this time the monthly sampling from July 1968 to June 1969 over four depth intervals extending down to 2000m.

Composition of the pelagic communities

A. Pelagic fishes

In a recent summary of the pelagic fishes caught during the 2006 Census of Marine Zooplankton cruise to the Sargasso Sea Sutton *et al* 2010 reported the collection of 127 species (84 genera) from 42 families. The numbers of fish captured per 105m^{3} declined from 112 in the upper 1000m to 0.2 at 4000-5000m (**FIG. 17**). Twenty-one taxa were only taken in the upper 1000m, and 24 taxa were only taken below 1000m. The most abundant fish was *Cyclothone braueri,* which contributed 47% of the catches <1000m and 41% >1000m, and its congeners *C. pallida* and *C. microdon*. Statistical analysis of the fish data separated the species into three assemblages two in the upper 1000m to the north and south of the subtropical convergence, and also the bathypelagic species from >1000m which appeared to form a single assemblage. Sutton classifies the bathypelagic fish fauna into three classes of species *viz* 1. spanners which have broad bathymetric distributions throughout much of the water column; 2. vacillators which occur between 800-1500m and which, either do not migrate on a diel basis such as *Serrivomer* and *Bathylagus,* or undertake diel migrations to depths >1000m such the myctophids *Notoscopelus* and *Ceratoscopelus*;and 3. holobathypelagic species that are seldom taken above 1000m, such as ceratioid anglers, eurypharyngid and saccopharyngid eels and Chiasmodontids.

DEPTH ZONE	STATION 1		STATION 2		STATION 3		STATION 4		STATION 5	
	S	H'	S	H'	S	H'	S	H'	S	H'
0-1000	4	1.29	10	2.28	9	2.12	8	2.03	9	2.03
1000-2000	13	2.48	nd	Nd	16	2.74	20	2.95	8	2.03
2000-3000	13	2.48	nd	Nd	3	1.08	0	0	8	2.03
3000-4000	Nd	nd	23	3.05	2	0.69	1	0	5	1.60
4000-5000	Nd	nd	nd	nd	0	0	1	0	19	2.89

TABLE 2. Indices of fish diversity within depths zones at five deep stations sampled during the CMarZ in the Sargasso Sea in 2006. S = species number; H' = Shannon diversity index (from Sutton et al., 2010)

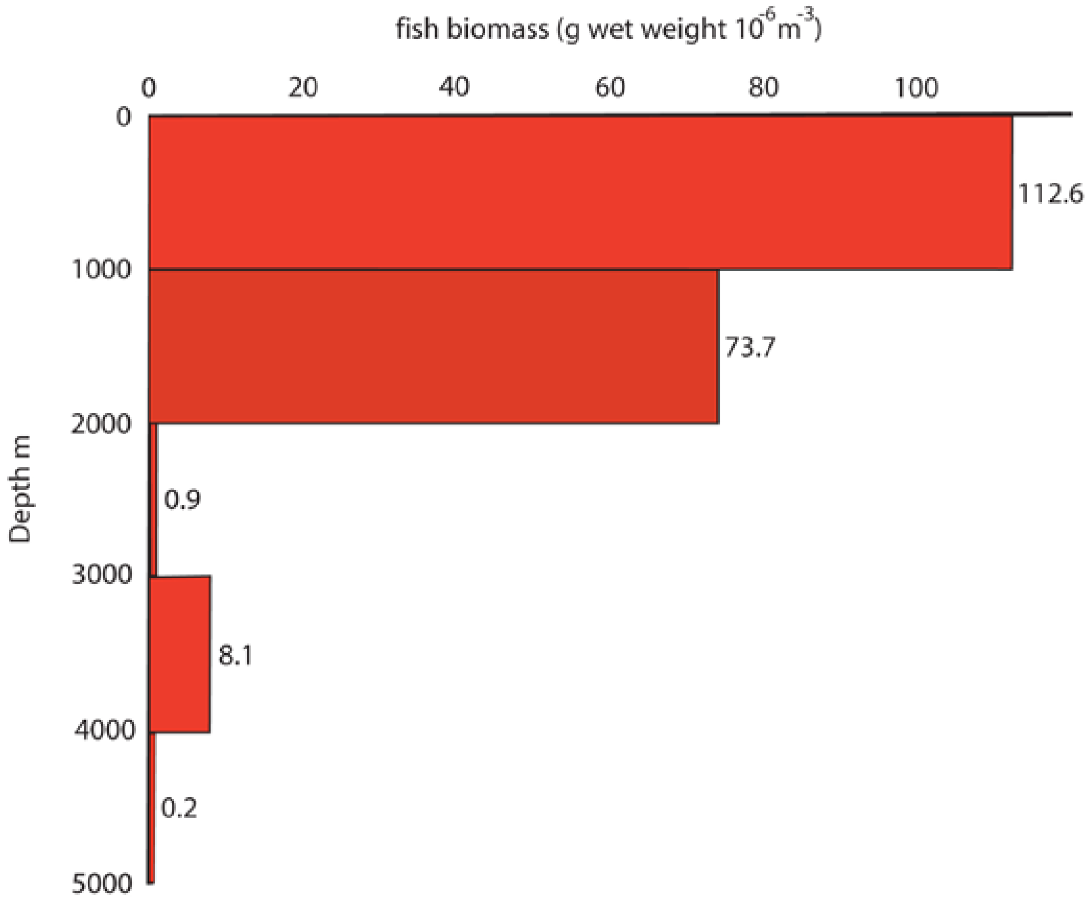


FIGURE 17. Mean biomass of fish (g wet weight/10^6m^3 between the surface and 5000m in the Sargasso Sea. (from Sutton et al., 2010).

The diversity of the midwater fish fauna in and around Ocean Acre is very rich. Gibbs and Krueger (1987) reporting on extensive trawling surveys to depths of 1500m of the fishes of Ocean Acre found 7 species of hatchet fishes (Sternoptychidae) (n=6800), 63 species of lantern fishes (Myctophidae) (n=47,000) and 15 species of big mouths (Melamphaidae) (n=4000). The zoogeography of the fishes in the North-west Atlantic is summed up in Backus et al., 1977, and the other volumes in this series give a uniquely detailed taxonomic summary of the fishes in the region.

B. Decapoda and Mysidacea

Rather surprisingly little has been published on the pelagic decapods and mysids, which contribute a fairly substantial proportion of the biomass of the micronekton. Donaldson (1975) reported on 14 species of sergestid shrimps that are such large and colourful members of the fauna in the upper 1000m of the water column off Bermuda. Some of the decapod species carry out diel vertical migrations over ranges of many hundreds of metres. Rather surprisingly the eucopid and gnathophausid mysids that are amongst the dominant members of the micronekton at depths of 1000-2000m do not feature much in the literature. Possibly partly because authors tend to focus on more speciose groups and partly because the recent trend is to study processes rather than the more classical approach of community analysis.

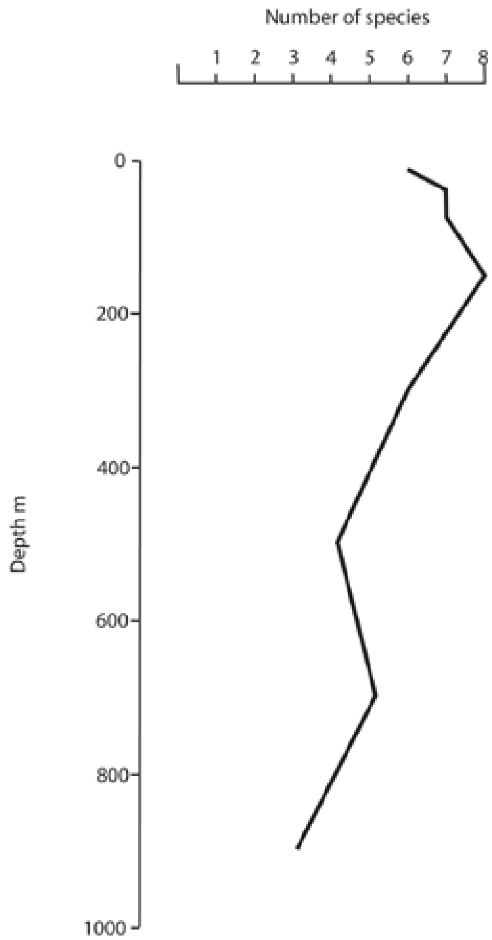


FIGURE 18. **Bathymetric profile of chaetognath species richness in the Sargasso Sea (from Pierrot-Bults and Nair, 2010).**

C. Chaetognatha

The Chaetognatha (or arrow worms) is a phylum that is unique to the marine environment. They are gelatinous worm-like animals, of which about 100 of the 140 species are pelagic. Despite being easily damaged in nets, they are predators, principally of copepods. They are ubiquitous in oceans and occur at all depths. They occur in highest abundances in the epipelagic zone. Pierrot-Bults and Nair (2010) report abundances in the upper 25m of the water column near Bermuda of up to 1900 m^{-2} (up to 80 m^{-3}) The epipelagic species are predominantly very small, whereas the deeper living species are far less abundant but are much larger. So although at depths of around 200-300m their abundances may be two orders of magnitude lower, their standing crop may be over double that in the upper 25m. Pierrot-Bults and Nair (2010) reported 17 species from the Sargasso Sea, of which 7 are predominantly epipelagic, 5 are mesopelagic, and 3 bathypelagic (**FIGURE 18**).

Cheney (1985a) reported finding 21 species, the difference being the seven species that occurred almost exclusively in the Slope Water, which occurs to the north west of the main flow of the Gulf Stream (see comments on the impact of mesoscale eddies). Cheney concludes that seven of the species are typical of Slope Water and nine are typical of the Northern Sargasso Sea, and when their species occur in the other water types they are expatriates advected in by the mesoscale eddies. He also concluded that only one species showed significant inter-seasonal variations in abundance in the Slope Water, but six showed significant seasonal variations in the Northern Sargasso Sea. Cheney (1985b) observed almost identical patterns in the depth distributions of the various species, but also observed that some of the species with mesopelagic daytime distributions undertook diel vertical migrations, notably *Sagitta maxima* and *Eukrohnia hamata*.

D. Gelatinous organisms

The great importance of gelatinous species in oceanic environments especially in low productivity regions (oligotrophic) went largely unrecognised until the advent of blue-water diving and the availability of *in situ* observations using submersibles, particularly along the east coast of the States. These species include both predators such as the medusae (Mills 1995), siphonophores (Purcell, 1981), and ctenophores (Harbison et al., 1978), and herbivorous species such as salps and larvaceans. The reason for this apparent oversight is that many of these species are extremely fragile and disintegrate either in nets or when being preserved (especially some of the Ctenophora). Many of the species form swarms and so their occurrence is highly patchy in space and time. Salps and some of the siphonophores form large 'colonies' which tend to fall apart in nets making accurate quantitative observations impossible to achieve using classical sampling techniques.

E. Hyperiid amphipods

Many of these are associated with gelatinous organisms especially when juvenile. Gasca (2007) recently reported finding 88 species in the upper 400m of the water column in the Sargasso Sea, which raised the know amphipod fauna of the region to 126. She comments that extending the sampling into deeper water would substantially increase the numbers of known species.

Impact of Gulf Stream Rings

A special feature of the Bermuda region is the occurrence of these rings. Formed by meanders in the main flow of the Gulf Stream, the typical diameter of a ring is 200km. There are two types of ring, warm core rings and cold core rings. Warm core rings form on the inshore side of the Gulf Stream and spin in a clockwise direction. They are analogous to high pressure anticyclones in the atmosphere, and have elevated sea-levels over their cores of warm water derived from the Sargasso Sea surrounded by a ring of Gulf Stream water. They move north and west through the Slope Water which is cool because inshore the currents are flowing from the north. Since they occur over the continental shelf they do not impact the seas around Bermuda. The cold core currents circulate cyclonically (anticlockwise) and contain a core of cool Slope Water ringed by Gulf Stream water and move through the warm waters of the Northern Sargasso Sea. When they first form they can be identified by the coolness of the surface water in their core. As they age, this surface temperature signature is lost, but they can still be identified by satellites fitted with altimeters that detect the lowering of the sea surface over their cores.

They have considerable biological significance because the Slope Water that gets entrained into their cores and the outer circulating ring of Gulf Stream water carry with them the pelagic organisms that are typical of each of these water masses. So organisms that are typical of the cool waters that normally lie over the slope are entrained and become expatriates into the Northern Sargasso Sea. The rings tend to drift south and west and many become re-entrained into the flow of the Gulf Stream. But a proportion do not move far enough westwards to become entrained back into the flow and some of these have been tracked with SOFAR floats for over a year. Gradually they become eroded by intermixing with the surrounding water. Because of the relatively high density of water, these eddies contain much more kinetic energy than their counterparts in the atmosphere, and their influence extends throughout the total water column. They interact with the seabed interface, creating 'benthic storms' that churn up the water overlying the sea-floor extending the benthic boundary layer up to a kilometre above the bottom. As a result organisms like the large necrophagous scavenging anphipods can occasionally be caught high up above the bottom, in contrast to the normal situation where baited traps set more than a few tens of metres above the bottom do not attract any of these amphipods.

Wiebe and Boyd (1978) and Wiebe and Flierl (1983) followed the fates of some of the euphausiid species that became entrained in eddies, and found that a range of different physical exchanges are occurring. The most important is horizontal mixing, which is minimal between 150-400m. A few warm water species were able to penetrate rings and exploit the changing ring conditions, but many, whether or not they are diel vertical migrators, penetrated the ring very slowly. Cold water species show varied responses to ring decay; *Thysanopoda longicaudata* disappears within 3-4 months, whereas *Nematoscelis megalops* and *Euphausia krohnii* persist for 6-12 months.

Fairbanks et al., (1980) estimated that 50-75% of the foraminiferan tests collected from the seabed in core samples in the Sargasso Sea were from expatriate species carried in by cold-core eddies. Their isotopic composition is used extensively by palaeontologists to reconstruct past sea surface temperatures, and the effect of the Gulf Stream rings is to extend the apparent record of the southern boundary of the cold water regime well to the south.

A number of papers have discussed the influence of the rings on mesopelagic fishes, particularly on the attractiveness of the bounding fronts (e.g. Backus *et al,* 1969, Backus and Craddock, 1982) and on the biomass of micronekton in general (Boyd et al., 1986).

The influence of the rings is summed up in Wiebe and Flierl (1983) who states:

"By virtue of the distribution of rings, there is in the North-western Atlantic Ocean, a mosaic pattern of expatriated communities interspersed throughout home-range communities. This pattern is continuously changing because of the horizontal movement of rings and because of hydrographic changes resulting from air-sea interactions and physical exchange processes with adjacent waters, which foster change in ring biotic structure towards that of the surrounding Sargasso Sea."

Conclusions

1. The only features of the mid-water ecology of the ocean around Bermuda that are in any way special are the influence of the Gulf Stream rings and the presence of the 18°C water. Otherwise its characteristics are typical of mid-latitude oligotrophic regions.
2. The region is probably the most thoroughly studied area of the global ocean, and there is considerable value to science in keeping it as pristine as possible.
3. It is a region of relatively low productivity, nevertheless it has a high species richness (biodiversity).
4. The BATS time series is a long time series of physical, chemical and biological oceanic observations. It constitutes a powerful scientific tool for monitoring, understanding and predicting oceanic responses to shifts and oscillations in climate.
5. The assemblages of pelagic species found within the deep water column in the Sargasso Sea are generally similar. to those found throughout the subtropical Atlantic

References

Angel, M.V. 1979. Studies on Atlantic halocyprid ostracods: Their vertical distributions and community structure in the central gyre region along latitude 30°N from off Africa to Bermuda. *Progress in Oceanography*, 8: 1–122.

Angel, M.V. and A. de C. Baker 1982. Vertical standing crop of plankton and micronekton at three stations in the Northeast Atlantic. *Biological Oceanography*, 2: 1–30.

Angel, M.V. and P.M. Hargreaves, 1992. Large-scale patterns in the distribution of planktonic and micronektonic biomass in the North-east Atlantic. *ICES J.mar.sci.* 49:403–411.

Angel, M.V. 2010. Towards a full inventory of planktonic Ostracoda (Crustacea) for the subtropical Northwestern Atlantic Ocean. *Deep-Sea Research II*, 57, 2173–2188.

Backus, R. H., J. E. Craddock, R. L. Haedrich and B. H. Robison, 1977. Atlantic mesopelagic zoogeography. In: Fishes of the Western North Atlantic. *Mem. Sears Found. Mar. Res.* 1(7): 266–287.

Backus, R. H. and J. E. Craddock, 1982. Mesopelagic fishes in Gulf Stream cold-core rings. *J. Mar. Res. 40 (Supplement)*: 1–20.

Backus, R.H., J.E. Craddock, R.L. Haedrich, and D.L. Shores, 1969. Mesopelagic fishes and thermal fronts in the western Sargasso Sea. *Marine Biology* 3: 87–106.

Boyd, S. H., P. H. Wiebe, R. H. Backus, J. E. Craddock and M. A. Daher, 1986. Biomass of the micronekton in Gulf Stream ring 82-B and environs: changes with time. Deep-Sea Res. 33: 1885–1905.

Brooks A.L. and R. Sanger, 1991. Vertical size-depth distribution properties of midwater fishes off Bermuda, with comparative reviews for other open ocean areas. *Can, J. Fish, Aquat. Sci.* 48: 694–721.

Cheney, J. Spatial and temporal abundance patterns of oceanic chaetognaths in the western North Atlantic–1. Hydrographic and seasonal abundance patterns. *Deep-Sea Res.*, 32: 1041–1059.

Cheney, J. Spatial and temporal abundance patterns of oceanic chaetognaths in the western North Atlantic–1l. Vertical distributions and migrations. *Deep-Sea Res.*, 32: 1061–1075.

Conte, M. H., J. K. B. Bishop and R. H. Backus, 1986. 12-kHz nonmigratory deep-scattering layers of Sargasso Sea origin in warm-core rings. *Deep-Sea Res.* 33: 1869–1884.

Countway, P.D., R.J.Gast, M.R. Dennett, P. Savai, J.M. Rose, and D.a Caron. 2007. Distinct protistan assemblages characterize the euphotic zone and deep sea (2500m) of the western North Atlantic (Sargasso Sea and Gulf Stream). *Environmental microbiology*, 9: 1219–1232.

Craddock, J.E., R.H. Backus, and M.A. Daher, 1992. Vertical distribution and species composition of midwater fishes in warm-core Gulf Stream meander/ring 82 H. *Deep-Sea Research* 39, suppl. 1: S203–S218.

Deevey, G.B. (1968). *Bathyconchoecia,* a new genus of pelagic ostracods (Myodocopa, Halocyprididae) with six new species from the deeper waters of the Gulf of Mexico. *Proceedings of the Biological Society of Washington,* 81: 539–570.

Deevey, G.B. 1971. The annual cycle in quantity and composition of the zooplankton population of the Sargasso Sea off Bermuda. Limnology and Oceanography, 16: 219–240.

Diekmann R. and U. Piatkowski, 2002. Early life history stages of cephalopods in the Sargasso Sea: Distribution and diversity relative to hydrographic features. *Marine Biology 141*: 123–130.

Donaldson, H.A. 1975. Vertical distribution of sergestid shrimps (Deacapoda, Natantia) collected near Bermuda. *Marine Biology*, 31: 37–50.

Fairbanks, R.G., P.H. Wiebe and AWH Bé, 1980, Vertical distribution and isotopic composition of living planktonic Foraminifera in the western North Atlantic. *Science*, 207: 61–63.

Gartner, J.V. P. Steele and J.J. Torres, 1989. Aspects of the distribution of lanternfishes (Pisces; Myctophidae) from the Northern Sargasso Sea. *Bull. Mar. Sci.*, 45: 555–563.

Gasca, R. 2007. Hyperiid amphipods of the Sargasso Sea. *Bulletin of Marine Science*, 81: 115–125.

Gibbs R.H. and W.H. Krueger, 1987. Biology of midwater fishes of the Bermuda Ocean acre. *Smithsonian Contributions to Zoology*, 452: 185pp.

Harbison G.R., L.P.Madin, and N.R.Swanberg, 1978. On the natural history and distributions of oceanic ctenophores. *Deep-Sea Research*, 25: 233–256.

McGillicuddy et al., 2007, Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms, *Science*, 316: 1021–1026.

Mills C.E. 1995. Medusae, siphonophores, and ctenophores ae planktivorous feeders in changing global ecosystems. *ICES J. Mar.Sci.*, 52: 575–581.

Nafpaktitis, B. H., R. H. Backus, J. E. Craddock, R. L. Haedrich, B. H. Robison and C. Karnella, 1977. Family Myctophidae. In: Fishes of the Western North Atlantic. *Mem. Sears Found. Mar. Res.* 1(7): 13–265.

Olson, D. B. and R. H. Backus, 1985. The concentrating of organisms at fronts: a cold-water fish and a warm-core Gulf Stream ring. *Jour. Mar. Res.* 43: 113–137.

Pierrot-Bults A.C. 1982. Vertical distribution of Chaetognatha in the central Northwest Atlantic near Bermuda. *Biological Oceanography*, 2: 31–61.

Pierrot-Bults A.C. and V.R.Nair, 2010. Horizontal and vertical distribution of Chaetognatha in the upper 1000m of the western Sargasso Sea and the central and South-east Atlantic. *Deep Sea Research II* 57: 2189–2198.

Piotkovski S.A. and C. Castellani, 2009. Long-term decling trend of zooplankton biomass in the tropical Atlantic. *Hydrobiologia*, 632: 365–370.

Purcell, J,E, 1981. Dietary composition and diel feeding patterns of epipelagic siphonophores. *Marine Biology*, 65: 83–90.

Shackleton, N.J. 1982. The deep-sea sediment record of climate variability. *Progress in Oceanography*, 11: 199–218.

Sutton, T.T., P.H. Wiebe, L. Madin, and Ann Bucklin, 2010. Diversity and community structure of pelagic fishes to 50000m depth in the Sargasso Sea. *Deep Sea Research II* 57: 2220–2233.

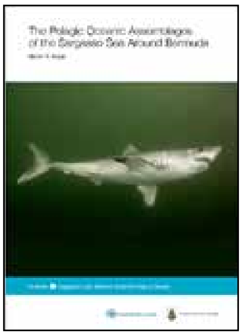
Wiebe, P.H. and G.R.Flierl 1983. Euphausiid invasion/dispersal in Gulf Stream Cold Core rings. *Aust. J. Mar. Freshw. Res.* 34: 625–652.

Woodd-Walker, R.S. 2001. Spatial distributions of copepod genera along the Atlantic Meridional. Transect. *Hydrobiologia*, 453/454: 161–170.

Woodd-Walker, R.S, P. Ward and A. Clarke 2002. Large-scale patterns in diversity and community structure of surface water copepods from the Atlantic Ocean. *Marine Ecology Progress Series*, 236: 189–203.

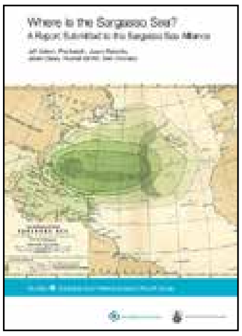
Sargasso Sea Alliance Science Series

The following is a list of the reports in the Sargasso Sea Alliance Science Series. All can be downloaded from www.sargassoalliance.org:



1

Angel, M.V. 2011. *The pelagic ocean assemblages of the Sargasso Sea around Bermuda.* Sargasso Sea Alliance Science Report Series, No 1, 25 pp.



2

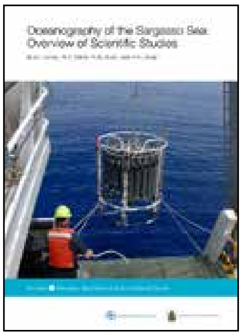
Ardron, J., Halpin, P., Roberts, J., Cleary, J., Moffitt, M. and J. Donnelly 2011. *Where is the Sargasso Sea?* Sargasso Sea Alliance Science Report Series, No 2, 24 pp.

3

Gollock, M. 2011. *European eel briefing note for Sargasso Sea Alliance.* Sargasso Sea Alliance Science Report Series, No 3, 11 pp.

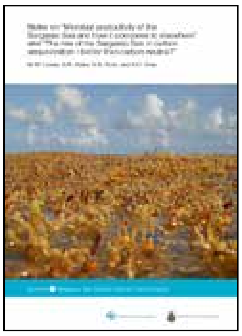
4

Hallett, J. 2011. *The importance of the Sargasso Sea and the offshore waters of the Bermudian Exclusive Economic Zone to Bermuda and its people. Sargasso Sea Alliance* Science Report Series, No 4, 18 pp.



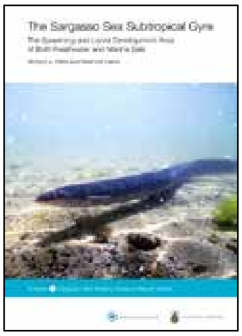
5

Lomas, M.W., Bates, N.R., Buck, K.N. and A.H. Knap. (eds) 2011a. *Oceanography of the Sargasso Sea: Overview of Scientific Studies.* Sargasso Sea Alliance Science Report Series, No 5, 64 pp.



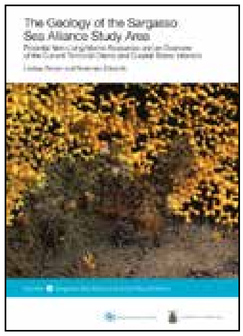
6

Lomas, M.W., Bates, N.R., Buck, K.N. and A.H. Knap. 2011b. *Notes on "Microbial productivity of the Sargasso Sea and how it compares to elsewhere" and "The role of the Sargasso Sea in carbon sequestration—better than carbon neutral?"* Sargasso Sea Alliance Science Report Series, No 6, 10 pp.



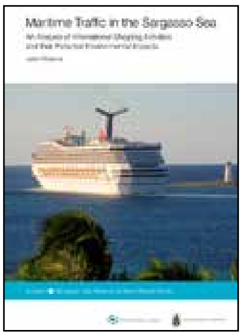
7

Miller, M.J. and R. Hanel. 2011. *The Sargasso Sea subtropical gyre: the spawning and larval development area of both freshwater and marine eels.* Sargasso Sea Alliance Science Report Series, No 7, 20 pp.



8

Parson, L. and R. Edwards 2011. *The geology of the Sargasso Sea Alliance Study Area, potential non-living marine resources and an overview of the current territorial claims and coastal states interests.* Sargasso Sea Alliance Science Report Series, No 8, 17 pp.

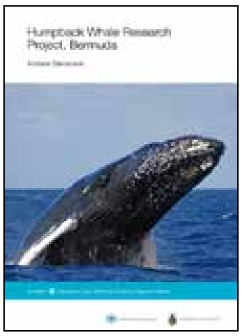


9

Roberts, J. 2011. *Maritime Traffic in the Sargasso Sea: An Analysis of International Shipping Activities and their Potential Environmental Impacts.* Sargasso Sea

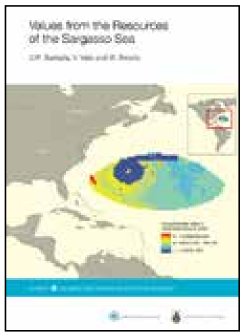
10

Siuda, A.N.S. 2011. *Summary of Sea Education Association long-term Sargasso Sea surface net data.* Sargasso Sea Alliance Science Report Series, No 10, 18 pp.



11

Stevenson, A. 2011. *Humpback Whale Research Project, Bermuda.* Sargasso Sea Alliance Science Report Series, No 11, 11 pp.



12

Sumaila, U. R., Vats, V., and W. Swartz. 2013. *Values from the resources of the Sargasso Sea.* Sargasso Sea Alliance Science Report Series, No 12, 24 pp.

SARGASSO SEA ALLIANCE

Since the initial meetings the partnership around the Sargasso Sea Alliance has expanded. Led by the Government of Bermuda, the Alliance now includes the following organisations.

PARTNER	TYPE OF ORGANISATION
Department of Environmental Protection	Government of Bermuda
Department of Conservation Services	Government of Bermuda
Mission Blue / Sylvia Earle Alliance	Non-Governmental Organisation
International Union for the Conservation of Nature (IUCN) and its World Commission on Protected Areas	Multi-lateral Conservation Organisation
Marine Conservation Institute	Non-Governmental Organisation
Woods Hole Oceanographic Institution	Academic
Bermuda Institute for Ocean Sciences	Academic
Bermuda Underwater Exploration Institute	Non-Governmental Organisation
World Wildlife Fund International	Non-Governmental Organisation
Atlantic Conservation Partnership	Non-Governmental Organisation