

Biogeography of the Oceans: a Review of Development of Knowledge of Currents, Fronts and Regional Boundaries from Sailing Ships in the Sixteenth Century to Satellite Remote Sensing

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Abstract—The development of knowledge of global biogeography of the oceans from sixteenth-century European voyages of exploration to present-day use of satellite remote sensing is reviewed in three parts; the pre-satellite era (1513–1977), the satellite era leading to a first global synthesis (1978–1998), and more recent studies since 1998. The Gulf Stream was first identified as a strong open-ocean feature in 1513 and by the eighteenth century, regular transatlantic voyages by sailing ships had established the general patterns of winds and circulation, enabling optimisation of passage times. Differences in water temperature, water colour and species of animals were recognised as important cues for navigation. Systematic collection of information from ships' logs enabled MAURY (The Physical Geography of the Sea Harper and Bros. New York 1855) to produce a chart of prevailing winds across the entire world's oceans, and by the early twentieth century the global surface ocean circulation that defines the major biogeographic regions was well-known. This information was further supplemented by data from large-scale plankton surveys. The launch of the Coastal Zone Color Scanner, specifically designed to study living marine resources on board the Nimbus 7 polar orbiting satellite in 1978, marked the advent of the satellite era. Over subsequent decades, correlation of satellite-derived sea surface temperature and chlorophyll data with in situ measurements enabled LONGHURST (Ecological Geography of the Sea. Academic Press, New York 1998) to divide the global ocean into 51 ecological provinces with Polar, Westerly Wind, Trade Wind and Coastal Biomes clearly recognisable from earlier subdivisions of the oceans. Satellite imagery with semi-synoptic images of large areas of the oceans greatly aided definition of boundaries between provinces. However, ocean boundaries are dynamic, varying from season to season and year to year. More recent work has focused on the study of variability of currents, fronts and eddies, which are often the focus of high biological productivity. Direct tracking of animals using satellite-based systems has helped resolve the biological function of such features and indeed animals instrumented in this way have helped the study of such features in three dimensions, including depths beyond the reach of conventional satellite remote sensing. Patterns of surface productivity detected by satellite remote sensing are reflected in deep sea life on the sea floor at abyssal depths >3,000 m. Satellite remote sensing has

played a major role in overcoming the problems of large spatial scales and variability in ocean dynamics and is now an essential tool for monitoring global change.

Key words: Oceans, biogeography, ocean colour, chlorophyll, CZCS.

1. Introduction

The aim of this review is to give a broad overview of the role that satellite technology has played in study of biogeography of the open ocean. This account is divided into three parts, the pre-satellite era (1513–1977), the satellite era leading to a first global synthesis (1978–1998) and more recent studies since 1998.

Ever since humans began making extended voyages on the oceans, from frozen polar seas to tropical coral archipelagos, it became evident that the environment and the organisms living there vary from place to place. With reference to the first law of geography, “everything is related to everything else, but near things are more related than distant things” (TOBLER 1970), biogeography is concerned with understanding differences in living communities or assemblages and their constituent species generally over large spatial scales. In terrestrial biogeography, by the early twentieth century, functionally similar major biotopes such as tropical rain forests had been recognised in different parts of the world but it was evident that the organisms making up the ecological communities could be taxonomically very different. Thus the forests of South America contain so-called New World monkeys (Platyrrhini), whereas similar forests in Africa and Asia are populated by Old World monkeys and

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apes (Catarrhini). In the forests of Northern Australia and adjacent islands south of the Wallace line there are no monkeys or apes (GROVES 2005). Therefore, biogeography is not entirely defined by the present-day physical environment that defines the biotope (e.g. tropical rain forests). Biogeography must include an understanding of the evolutionary and environmental history of the location that determines the species inhabiting the area (e.g. whether there are primates). However, living organisms themselves play a role as environmental architects or ecosystem engineers modifying the environment (JONES *et al.* 1994). Large forest trees create habitat for numerous species that could not otherwise survive in the area. Indeed oxygen in the atmosphere originated from biological photosynthesis creating the conditions for life on earth as we know it (DAHL *et al.* 2010). Thus biogeography is inextricably linked to understanding the history of the planet and the evolution of life upon it (ROSEN 1975)

For oceanic biogeography it has been more difficult to attain a synthesis than for the terrestrial environment. The deep sea remains poorly understood in terms of biodiversity; exploration is a slow, painstaking process of retrieving samples from great depths (average depth 3,800 m), and indeed the deepest point of the world's oceans (ca. 11 km) has only been reached twice by manned vehicles and on neither occasion were meaningful biological samples obtained (JAMIESON and YANCEY 2012). The open ocean is a dynamic, fluid environment with a lack of obvious fixed boundaries on the surface. However, currents, fronts, gyres and eddies with contrast between waters of different temperatures or densities can be as distinct as biogeographic frontiers on land. Often such features are marked by conspicuous animals such as whales and birds exploiting them as cues for navigation or enhanced feeding opportunities. Biogeographic structure in the ocean is therefore inextricably linked to an understanding of circulation patterns and prevailing winds. The history of the ocean biogeography thus coincides with the evolution of knowledge of atmospheric and oceanic circulation. It is in this context that this review from the sixteenth century onwards is presented.

2. The Pre-Satellite Era: 1513–1977

From the European perspective, an understanding of the global ocean began with the great voyages of discovery in the latter half of the fifteenth century. By the early sixteenth century, colonies had been established in the Americas and on 22 April 1513, Juan Ponce de León recorded during a voyage to Florida the presence of “*A current such that, although they had great wind, they could not proceed forward, but backward.....the current was more powerful than the wind*”. Ponce de León, as the governor of Puerto Rico, immediately appreciated the significance of knowledge of currents in the oceans for navigation. He is generally credited with the discovery of what is now known as the Gulf Stream. Over subsequent centuries through a gradual process of accumulation of information, the realisation emerged that oceans are not simple basins full of water but rather bodies having geographic features with boundaries and localised features. By 1770, Benjamin Franklin together with his cousin Timothy Folger, a whaling captain, published a chart of the Gulf Stream. They showed the general pattern of circulation now familiar in the North Atlantic with a westward flowing Gulf Stream in the north and a return current near the equator. Ships that made use of these currents could greatly reduce their passage times. The chart was generally ignored at the time and was only rediscovered in the early twenty-first century by RICHARDSON (2008), but there is no doubt that such information was recorded in ships' logs and used to advantage by knowledgeable navigators. Franklin noted that the speed of the current could be up to 10–12 km h⁻¹, and was recognisable by differences in water temperature, water colour and occurrence of different species of fishes and other marine animals. The importance of the regular pattern of trade winds in planning long distance voyages on the oceans was widely appreciated. The causes were vigorously debated (PERSSON 2006) leading HADLEY (1735) to formulate the now generally accepted theory of interaction between solar heating of the atmosphere in the tropics and the effect of the earth's rotation.

It took the organisational capabilities of the world's navies to start systematically documenting information from ships' logs. A pioneer in this

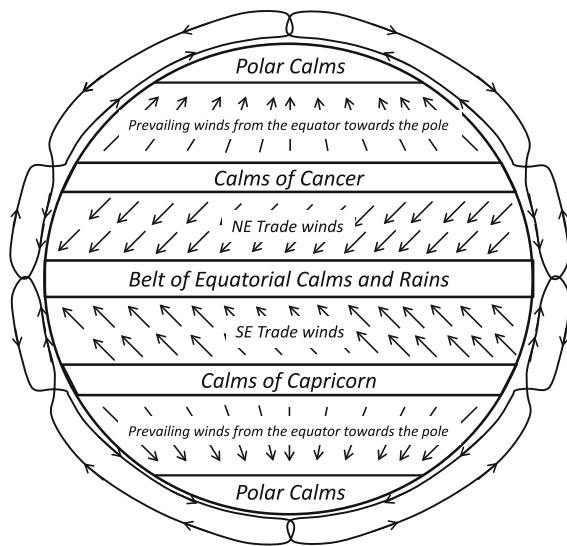


Figure 1

Diagram of wind patterns across the globe redrawn from plate I in MAURY (1855). The original caption was “Diagram of the winds”. Arrows around the globe indicate putative vertical air circulation in what are now known as Hadley cells

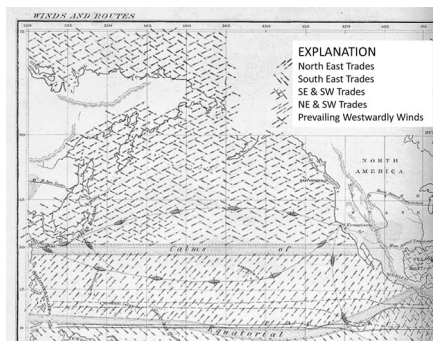


Figure 2

Part of the chart of the world's oceans showing winds and routes from plate VIII in MAURY (1855). The North Pacific Ocean is shown, indicating optimal routes for voyages by sailing vessels between San Francisco, California and Shanghai in China

respect was Matthew Fontaine Maury of the US Navy who began by collating weather information from US Navy ships. This culminated in a chart of prevailing wind patterns across the entire world's oceans (MAURY 1855) showing alternating bands of trade winds and calms in both the northern and southern hemisphere (Fig. 1). For the North Pacific Ocean (Fig. 2) he showed how a vessel making judicious use of these trade winds could reduce the passage time between the USA and China by 30 %. Regarding the

North Atlantic, Maury wrote “*There is a river in the ocean. In the severest droughts it never fails, and in the mightiest floods it never overflows. Its banks and its bottom are of cold water, while its current is of warm. The Gulf of Mexico is its fountain, and its mouth is in the Arctic Sea. It is the Gulf Stream*”. He also showed charts of the general patterns of ocean currents and indicated the polar limits of the sperm whales and the equatorial limits of right whales; an early exposition of global oceanic biogeography. Syntheses such as this led to international collaboration in gathering oceanographic and meteorological data for mutual benefit. By the twentieth century, with steam ships plying regular routes across the oceans, the general pattern of global surface ocean circulation as depicted in Fig. 3 had become well-known and was linked to the patterns of air circulation with easterly trades between the equator and 30°, westerlies between 30° and 60°, and polar circulation above 60° in both hemispheres. The general pattern of circulation is clearly modified by the presence of continents with circumpolar circulation only possible in the southern hemisphere. The Antarctic Ocean is therefore a geographically distinct area demarcated by the sub-antarctic front with a separate fauna to the south. Amongst the species, fishes, sharks and the cod family are essentially absent and their role as large predatory fishes is taken by notothenioids, which have uniquely evolved in the Antarctic from perciform ancestors (KOCK 1992). Several species of notothenioids have antifreeze glycoproteins (AFGPs) in their blood and tissue fluids enabling them to survive at temperatures below 0 °C (CHEN *et al.* 1997). The boundaries between circulation gyres in the oceans therefore can act as biogeographic barriers defining areas occupied by species evolutionarily adapted to different conditions.

An important development paralleling the advances in physical oceanography was the Continuous Plankton Recorder (CPR), which first logged more than 1,300 miles during the Discovery expedition to the Antarctic in 1925–26, detecting marked differences in abundance of plankton in different water masses (HARDY 1926). CPRs are towed behind research vessels or ships of opportunity and are designed to operate at normal passage speed, in contrast to the slow speed of conventional plankton

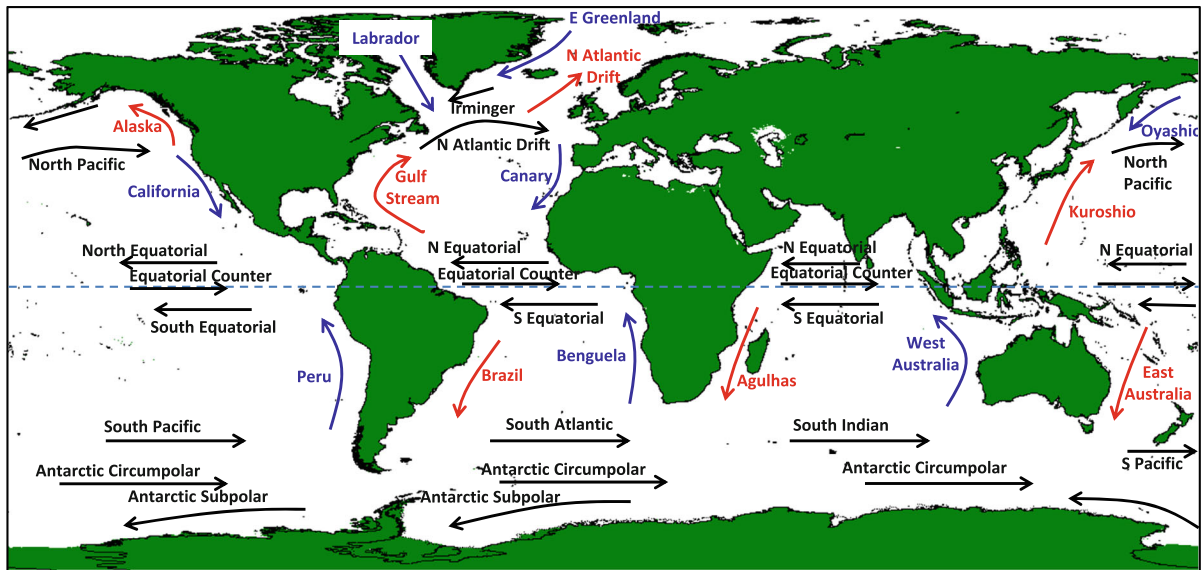


Figure 3

The general pattern of surface currents in the world's oceans. Drawn using GEBCO Centenary edition (2003) for coastal outlines. Location and naming of currents are based on PINET (1998) and other texts. *Red arrows* indicate currents transporting warm water to high latitudes, *Blue arrows* indicate currents transporting cold water to low latitudes. *Black currents* are parallel to lines of latitude

nets. The body of the CPR undulates up and downwards to sample the entire water-column depth of interest; small planktonic organisms are trapped on strip of silk mesh that moves like photographic film spooling through a camera, capturing a continuous sample along the ship's track. The spools have to be unrolled, organisms counted and identified by human operators; a skilled task requiring much patience and practise. CPR systems have been deployed around the world and the cumulative database now represents a major resource for studies on global change and how it is represented in the upper ocean (REID *et al.* 2003). TAYLOR and STEPHENS (1980) were able to show how the distribution of plankton in the North Atlantic changed between 1966 and 1977 in relation to changes in position of the north wall of the Gulf Stream and its associated eddies.

Based on the CPR and other systematic plankton surveys, several attempts were made to map regional differences in plankton species distribution in the Pacific Ocean, (BRINTON 1962) and the North Atlantic (Edinburgh Oceanographic Laboratory 1973). These studies continue to be important and are updated from time to time (BEAUGRAND 2004, CPR Survey Team 2004). In 2011, the Global Alliance of Continuous Plankton Recorder Surveys (GACS) was formed to

implement such programmes world-wide (<http://www.globalcpr.org/> accessed 21 July 2013).

3. The Satellite Era Leading to a First Global Synthesis (1978–1998)

It can be argued that ecological studies using remote sensing from satellites began on 24 October 1978 with the launch of the Coastal Zone Color Scanner (CZCS) instrument on board the Nimbus 7 polar orbiting satellite (PRIEDE 1983). HOVIS *et al.* (1980) described the CZCS as “*the only sensor in orbit that is specifically designed to study living marine resources*”. It was a proof of concept instrument intended to last no more than 12 months but in fact it continued operating until June 1986, far exceeding expectations in both performance and duration of operation. The CZCS was a multispectral scanner with two main bands for detection of chlorophyll plus reference bands (Table 1) and had a radiometric sensitivity 60 times higher than the contemporary Landsat multispectral scanner. Early success in mapping offshore concentrations of chlorophyll was demonstrated by publication of an image from 2 November 1978 showing remarkable

Table 1

Coastal Zone Color Scanner (CZCS) multispectral scanner bands
(Hovis *et al.* 1980)

Channel number	Wavelength	Purpose
1	433–453 nm	Chlorophyll (low concentration)
2	510–530 nm	Reference
3	540–560 nm	Chlorophyll (high concentration)
4	660–680 nm	Gelbstoffe
5	700–800 nm	Surface vegetation
6	10.5–12.5 μm	Surface temperature (infra-red)

spatial structure in the distribution of pigments across the Gulf of Mexico (HOVIS *et al.* 1980). Although the colour scale depicting chlorophyll plus phaeopigment concentration was calibrated in increments of 0.05 mg m^{-3} from 0.05 to $>1.00 \text{ mg m}^{-3}$, comparisons with in situ simultaneous surface measurements from a ship indicated agreement within 0.5 log pigment concentration (GORDON *et al.* 1980). Satellite-derived chlorophyll concentration images such as these have now been widely reproduced and are a familiar feature of any discussions of ocean biological productivity (FELDMAN *et al.* 1989). A global image is reproduced in Fig. 4. No immediate successor had been planned for CZCS and it was not until the launch of SeaWiFS (Sea-viewing Wide Field-of-view Sensor) in 1997 that a routine service of ocean colour data began to be provided by the USA. In the intervening period, missions from Japan (Marine Observation Satellite, MOS-1, launched in

1987. OCTS Ocean Color Temperature Scanner, 1996) and France (POLDER, POLARization and Directionality of the Earth's Reflectances, 1996) provided a service. Since the beginning of the twenty-first century in addition to SeaWiFS, satellite oceanography data have been provided by an increasing number of satellite sensors including MERIS (MEdium Resolution Imaging Spectrometer), carried on the European Space Agency, Envisat-1, launched in 2002 (BÉZY *et al.* 2000), and the Aquarius microwave sea surface salinity sensor on board the Argentine SAC-D spacecraft, launched in 2011.

The Nimbus satellite had limited power capabilities so not all sensors could be operated at all times. Furthermore, collection of data depended on a network of ground stations around the world collecting data in real time or delayed transmission from onboard magnetic tape recorders for parts of the orbit when the satellite was beyond the range of any ground station. The swath width of the CZCS was 1,600 km, and with 13.82 orbits per day the distance between successive equator crossings was 2,900 km, leaving gaps in the coverage in the tropics between successive orbits. The satellite was heliosynchronous with the day-time equator crossing at noon and a night-time crossing at midnight (irrelevant for the CZCS). Since the orbit number per day was not an integer (PRIEDE 1983), the NIMBUS did not follow the same track every day and could fill in gaps between the previous orbits until it returned to its

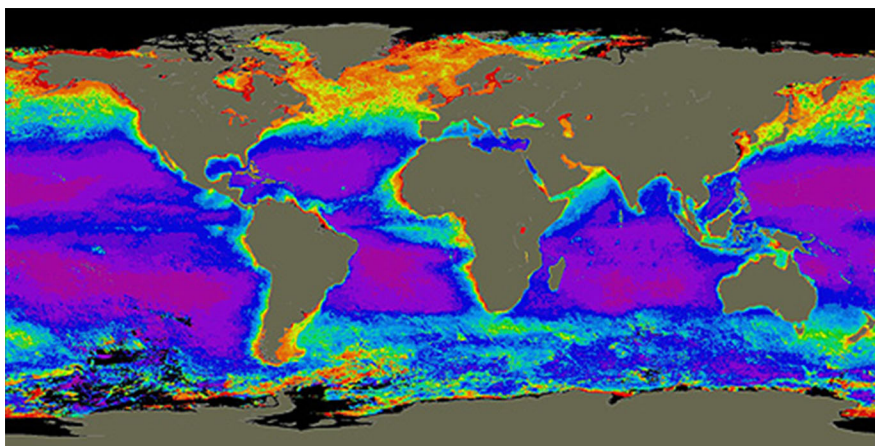


Figure 4

Global sea surface chlorophyll pigment concentration averaged over operational duration of the CZCS between 1978 and 1986. The image is in false colour with red denoting 10 mg m^{-3} and violet $<0.01 \text{ mg m}^{-3}$. Image from NASA/GSFC-DAAC (FELDMAN *et al.* 1989)

starting position every 6 days. Even in the early data analysis (GORDON *et al.* 1980) the noisiness of the data from the coarse digitisation (8 bit, $2^8 = 256$ increments) in the CZCS was commented upon. With the current ubiquity of computing power and routine digitisation of images it is difficult to appreciate the magnitude of the achievement in realising the CZCS during the 1970s. These constraints meant that the ideal of complete global coverage with ocean colour data every 24 h was not possible. In any case, large areas of the globe at any one time are covered with cloud; indeed, at mid-latitudes in the North Atlantic cloud-free views are a rarity. In the 1970s the scientific community was not ready for the volume of data produced by the CZCS but images of plankton blooms and their variability were very influential. The theoretical basis was already in place (YENTSCH 1965). Initially, the NASA Goddard Space Flight Center released interesting images but gradually systematic processing of global data progressed to the point that monthly mean data on a 1° grid became available for the years 1978–1986 on a global basis as well as in individual scenes at 4-km resolution. Chlorophyll values were computed using standard NASA algorithms based on HOVIS *et al.* (1980) and GORDON *et al.* (1980), which use the blue/green ratios at 433/550 nm wavelength for low chlorophyll concentrations and 520/550 nm for high chlorophyll concentrations with an accuracy of 35 % in the open ocean (FELDMAN *et al.* 1989). However there remains wide debate about the global validity of this algorithm (TILSTONE *et al.* 2009).

Viewing of the CZCS chlorophyll data, plus availability of corresponding sea surface temperature (SST) data and altimetry began to provide a tool for defining areas of the ocean with different biological characteristics. This was undertaken in a systematic way by LONGHURST (1998) in his seminal work “*Ecological Geography of the Sea*” who used the CZCS database, computing chlorophyll values according to SATHYENDRANATH and PLATT (1989). A powerful feature of Longhurst’s analysis is incorporation of data from 26,532 chlorophyll profiles obtained from archived data collected by ships. These were parameterised according to: depth of the chlorophyll maximum (Z_m m), the standard deviation around the peak value (s , m), the total pigment within

the peak (h , mg chlorophyll m^{-2}), the ratio (r') of peak height (value of chlorophyll maximum) to total pigment, and background chlorophyll concentration (B_o , mg chlorophyll m^{-3}). Ecological provinces were then defined in two steps. Examination of the surface CZCS chlorophyll field in different seasons and using different formats to locate boundaries was followed by study of oceanographic data for all the relevant regions. Eventually 51 putative provinces were identified, the boundaries of which were then tested using the archive of parameterised chlorophyll depth profiles. The approach used was to examine the frequency distribution of depth of the chlorophyll maximum, Z_m for all profiles within a candidate province. If the frequency distribution was bimodal or multimodal it was assumed the data did not represent a homogeneous region. The boundaries were then shifted until the distribution was unimodal and then the province boundaries were accepted. Seasonal variation can also create bimodal distributions but in practise a satisfactory solution was always found by small adjustment to boundaries. Statistical tests were then applied to determine the significance of differences between adjacent provinces, finally confirming the validity of the proposed boundaries. Changes in CZCS images during ENSO (El Niño Southern Oscillation) events were examined but there was no support for inter-annual alteration of boundaries of the Pacific Equatorial Divergence Province. This may have been due to incomplete seasonal coverage by the CZCS even in 90-day composite images.

Following this exhaustive process, LONGHURST (1998) proposed division of the oceans into 12 Biomes; for each ocean these are the Polar, Westerly Wind, Trade Wind and Coastal Biomes (Fig. 5). These are further subdivided to give 51 provinces (Table 2). Boundaries between the provinces are specified by straight longitudinal and latitudinal lines at a resolution of 1° (Fig. 6), the co-ordinates of which can now be downloaded from a number of sources (VLIZ 2009) for use in GIS and other mapping applications. The advantage of this scheme is that the areas are clearly identified and reproducible. LONGHURST (1998) furthermore provides a narrative description of each province together with graphs of monthly data showing the typical annual cycle in important variables such as mixed-layer depth, photic

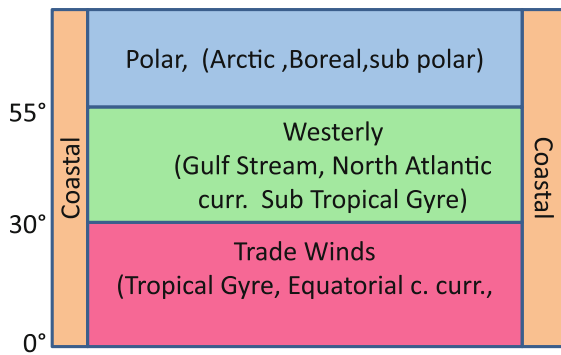


Figure 5

Diagrammatic representation of biomes according to LONGHURST (1998) in an oceanic hemisphere (e.g. North Atlantic). Strips on either side represent the Coastal Biomes. Approximate latitudes (north or south) are inserted on the left-hand side of the diagram

depth, chlorophyll-a concentration, and primary production (integrated over the depth profile and at the deep chlorophyll maximum DCM). Each province is identified by a four-letter acronym and these have become a widely-used shorthand for describing the habitat in different parts of the ocean. It should be emphasised that whilst satellite remote sensing played a crucial role in defining the areal extent of the provinces, the scheme is supported by a large database of sea-surface and sub-surface measurements.

4. Beyond the 1998 Global Synthesis; New Biogeographic Classifications, Variability and Tracking of Animals

Following the LONGHURST (1998) synthesis the need for global mapping of ocean habitats as a tool for management has been recognised at the political level and under the auspices of the United Nations Environment Program, Convention on Biodiversity and the Intergovernmental Oceanographic Commission has published the *Global Open Oceans and Deep Seabed Biogeographic Classification* (GOODS) (UNESCO 2009) which gives a useful overview of different approaches to biogeographic mapping of the high seas. Different maps are required for different purposes. VIERROS *et al.* (2009) present a map of pelagic provinces which is similar to that of LONGHURST (1998) but is simplified by combining eastern and western trade-wind provinces in each ocean and

coastal biomes are omitted since they are treated separately. Whereas the LONGHURST (1998) provinces have clear fixed boundaries the GOODS map is difficult to use since the precise latitudes and longitudes of the boundaries are not specified indeed the authors state “*The exact boundaries on the pelagic biogeographic map will remain work in progress... A major difference (from terrestrial biogeography) is that pelagic conservation approaches must deal with shifting ocean boundaries and large generalised provinces*”. It seems the limits have been reached of what is possible in pelagic biogeography in defining fixed boundaries analogous to those in terrestrial biogeography. Future studies must address the problem of shifting boundaries and some progress has been made in remote sensing detection of dynamic boundaries of provinces (DEVRED *et al.* 2007).

The problem of boundaries in oceans is compounded by the observation that highest energy dissipation (D’ASARO *et al.* 2011) and biological productivity tends to occur along fronts at the boundary between waters of different temperatures. Using satellite imagery of the North West Atlantic in the region of the Grand Banks, TAYLOR and FERRARI (2011) showed that chlorophyll concentration is higher along a front than in either of the surrounding water masses. In the Northwest Atlantic an important phenomenon is the formation of Gulf Stream Rings. These are created when meanders in the Gulf Stream are shed as eddies of rotating low density water floating in surrounding denser cold water. Rotation is cyclonic to the south of the stream and anti-cyclonic to the north. Such rings are often responsible for bringing anomalously warm water close to the shore of the Northeast USA or conversely carrying water from the continental slopes a long distance offshore. One such eddy was followed with the aid of satellite tracked buoys from its formation in February 1977 until it was reabsorbed by the Gulf Stream in September 1977 (RICHARDSON 1980). Eddies are often rich in biological productivity with high chlorophyll concentrations. Using the wider field capability of SeaWiFS sensors to map chlorophyll combined with sea surface altimetry and ship-borne measurements, PINGREE (2002) and PINGREE and GARCIA-SOTO (2004) investigated the formation and movement of eddies in different parts of the Northeast Atlantic Ocean. They

Table 2

List of Biomes and Provinces proposed by LONGHURST (1998)

	Ocean	Biome	Province			
1	Antarctic	1. Antarctic Polar	ANTA	Antarctic		
2			APLR	Austral Polar		
3		2. Antarctic Westerly Winds	SANT	Subantarctic Water Ring		
4			SSTC	South Subtropical Convergence		
5	Atlantic	3. Atlantic Coastal	BENG	Benguala Current		
6			BRAZ	Brazil Current		
7			CNRY	Eastern (Canary) Coastal		
8			FKLD	Southwest Atlantic Shelves		
9			GUIA	Guianas Coastal		
10			GUIN	Guinea Current Coastal		
11			NECS	Northeast Atlantic Shelves		
12			NWCS	Northwest Atlantic Shelves		
13				4. Atlantic Polar	ARCT	Atlantic Arctic
14					BPLR	Boreal Polar
15				SARC	Atlantic Subarctic	
16				5. Atlantic Trade Wind	CARB	Caribbean
17		ETRA	Eastern Tropical Atlantic			
18		NATR	North Atlantic Tropical Gyral			
19		SATL	South Atlantic Gyral			
20		6. Atlantic Westerly Winds	WTRA	Western Tropical Atlantic Province		
21			GFST	Gulf Stream		
22			MEDI	Mediterranean Sea Black Sea		
23			NADR	North Atlantic Drift		
24			NAST	North Atlantic Subtropical Gyral		
25	Indian		7. Indian Ocean Coastal	ARAB	Northwestern Arabian Upwelling	
26		AUSW		Australia-Indonesia Coastal		
27		EAFR		Eastern Africa Coastal		
28		INDE		Eastern India Coastal		
29		INDW		Western India Coastal		
30		REDS		Red Sea, Persian Gulf		
31		8. Indian Ocean Trade Wind	ISSG	Indian South Subtropical Gyre		
32			MONS	Indian Monsoon Gyres		
33	Pacific	9. Pacific Coastal	ALSK	Alaska Downwelling Coastal		
34			AUSE	East Australian Coastal		
35			CALC	California Current Province		
36			CAMR	Central American Coastal		
37			CHIN	China Sea Coastal		
38			HUMB	Humbolt Current Coastal		
39			NEWZ	New Zealand Coastal		
40			SUND	Sunda-Arafura Shelves		
41				10. Pacific Polar	BERS	North Pacific Epicontinental Sea
42					ARCH	Archipelagic Deep Basins
43		11. Pacific Trade Wind	NPTG	North Pacific Tropical Gyre		
44			PEQD	Pacific Equatorial Divergence		
45		PNEC	North Pacific Equatorial Countercurrent			
46		SPSG	South Pacific Subtropical Gyre			
47		12. Pacific Westerly Winds	WARM	Western Pacific Warm Pool		
48			KURO	Kuroshio Current		
49			NPPF	North Pacific Transition Zone Province		
50			PSAG	Pacific Subarctic Gyres (East & West)		
51			TASM	Tasman Sea		

discriminated several distinctive types of eddy at different latitudes: 24–27°N SWESTY Shallow Subtropical Anticyclonic Westward Propagating Eddy,

30–34°N STORM Subtropical Ocean Ring of Magnitude that also moves westwards, 35–37°N MEDDY Mediterranean core water eddy, and 44–52°N

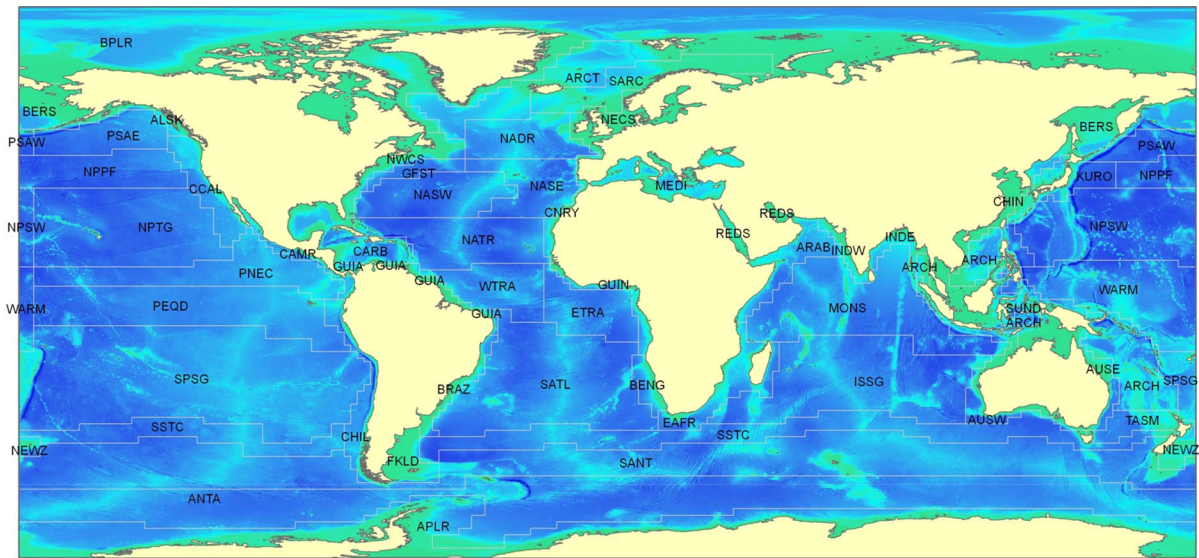


Figure 6

Oceanic ecological provinces defined by LONGHURST (1998) superimposed on bathymetry of the oceans. Figure prepared by Dr Toyo Fujii (Oceanlab, University of Aberdeen) using province boundaries downloaded from VLIZ (2009) and bathymetry from General Bathymetric Chart of the Oceans (GEBCO)

SWODDIES Slope Water Oceanic Eddies. MCGILLICUDDY *et al.* (2007) show that eddies potentially account for a large proportion of primary production in the oceans through a number of mechanisms that bring nutrient-rich waters to the surface (SIEGEL *et al.* 2011). Eddies are rather persistent dynamic features carrying the signature (in terms of salinity, temperature, nutrients, plankton, etc.) of water from distant sites of origin and acting as moving islands of biological productivity.

The dynamic nature of fronts and eddies limits the usefulness of conventional cartographic methods with fixed views in time and space. One solution has been to use a probabilistic approach. A first step is automated detection of fronts whereby an edge-detection algorithm is applied to single remote sensing images derived from the AVHRR (Advanced Very High Resolution Radiometer) to identify locations where sea surface temperature difference between two adjacent water masses exceeds a certain threshold; typically 0.2–0.4 K (MILLER 2009). This technique generates a series of lines on the image indicating the locations of fronts. However, in typical conditions at European high latitudes, only fragments of the sea surface can be seen through cloud cover in any given image. Therefore, composite images are constructed,

superimposing data from up to 3 days for thermal imagery. The same techniques can be applied to SeaWiFS chlorophyll maps but owing to the lower frequency of satellite overpasses, 5-day composites are used, the aim being to use as short a period of integration as possible to avoid loss of dynamic features. MILLER (2009) generated composite maps using three algorithms to estimate, F_{mean} the mean gradient from all fronts observed in a given pixel, P_{front} the probability of a front occurring in a given location, and F_{prox} a measure of proximity to the nearest neighbouring frontal feature. These three measures were combined with appropriate weightings to generate maps of presence of fronts. This technique successfully identified mesoscale eddies off the Iberian margin as described by PINGREE and LECANN (1992). The method can further be enhanced by incorporation of data from the Advanced Microwave Scanning Radiometer for EOS (AMSR-E), capable of detecting thermal fronts through cloud cover albeit at lower spatial resolution (25 km) compared with 1–4 km for the AVHRR. These approaches have been extended by MILLER and CHRISTODOULOU (in press) to produce seasonal maps of frequency of occurrence of fronts (Fig. 7). The regions of high probability of front occurrence are remarkably well-defined,

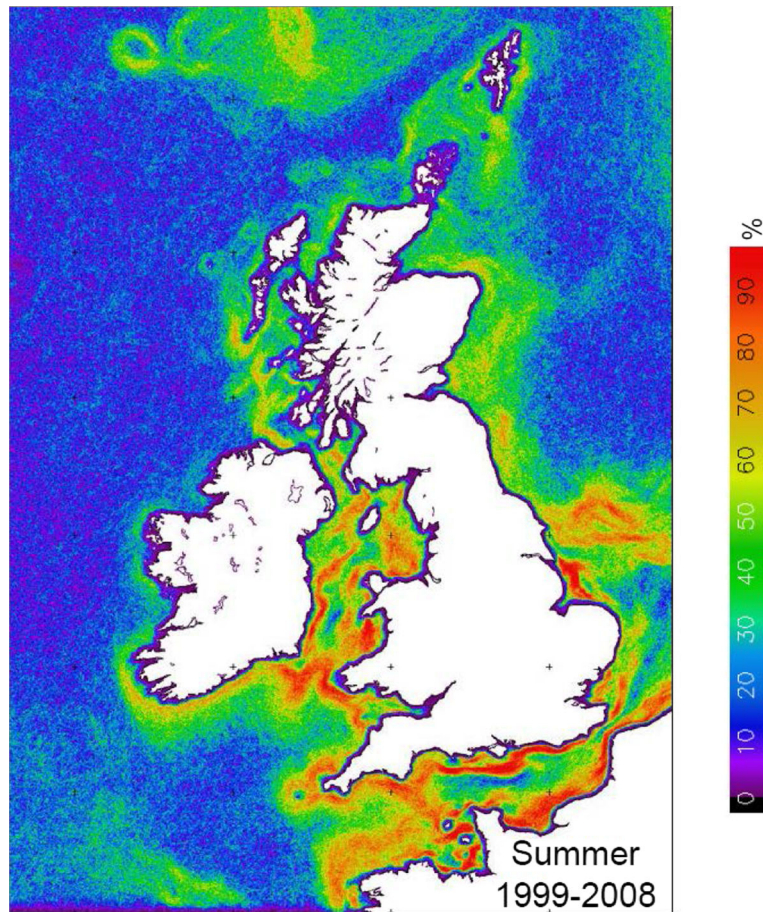


Figure 7

Map of frequency of fronts during summer time around the British Isles for the years 1999–2008 derived by applying front detection algorithms to combined infra-red and microwave wavelength satellite radiometer data (after MILLER and CHRISTODOULOU, unpublished image reproduced with permission of PETER MILLER, Remote Sensing Group, Plymouth Marine Laboratory, UK)

enabling such maps to be used for purposes of marine planning for management of fisheries, offshore renewable energy installations and other applications. The same techniques can be applied to produce ocean basin and global scale charts of distribution of fronts (MILLER *et al.* 2013) (P. Miller personal communication, Remote Sensing Group, Plymouth Marine Laboratory).

Whilst satellite remote sensing has provided the means of identifying different regions of the oceans based on physical parameters and ocean colour, the ultimate aim of biogeography is to understand the distribution of different species of marine organisms. An alternative approach therefore is to map the movements of animals directly. Early in the satellite era, success was achieved with simultaneously

imaging the sea surface temperature regime and tracking of a basking shark *Cetorhinus maximus* (PRIEDE 1984). The shark was equipped with an ARGOS beacon derived from the technology for tracking of sea surface data buoys such as used by RICHARDSON (1980) for the studies on Gulf Stream Rings. The basking shark with an adult weight of ca. 7 t was chosen as large enough subject for such studies since it could carry the relatively large transmitter pod. PRIEDE and MILLER (2009) demonstrated that in this pioneering study the shark was following the course of an offshore front detected by the automated front detecting algorithm (Fig. 8). With advances in technology making the transmitter packages smaller and lighter, it has become possible to track many different species of marine animals

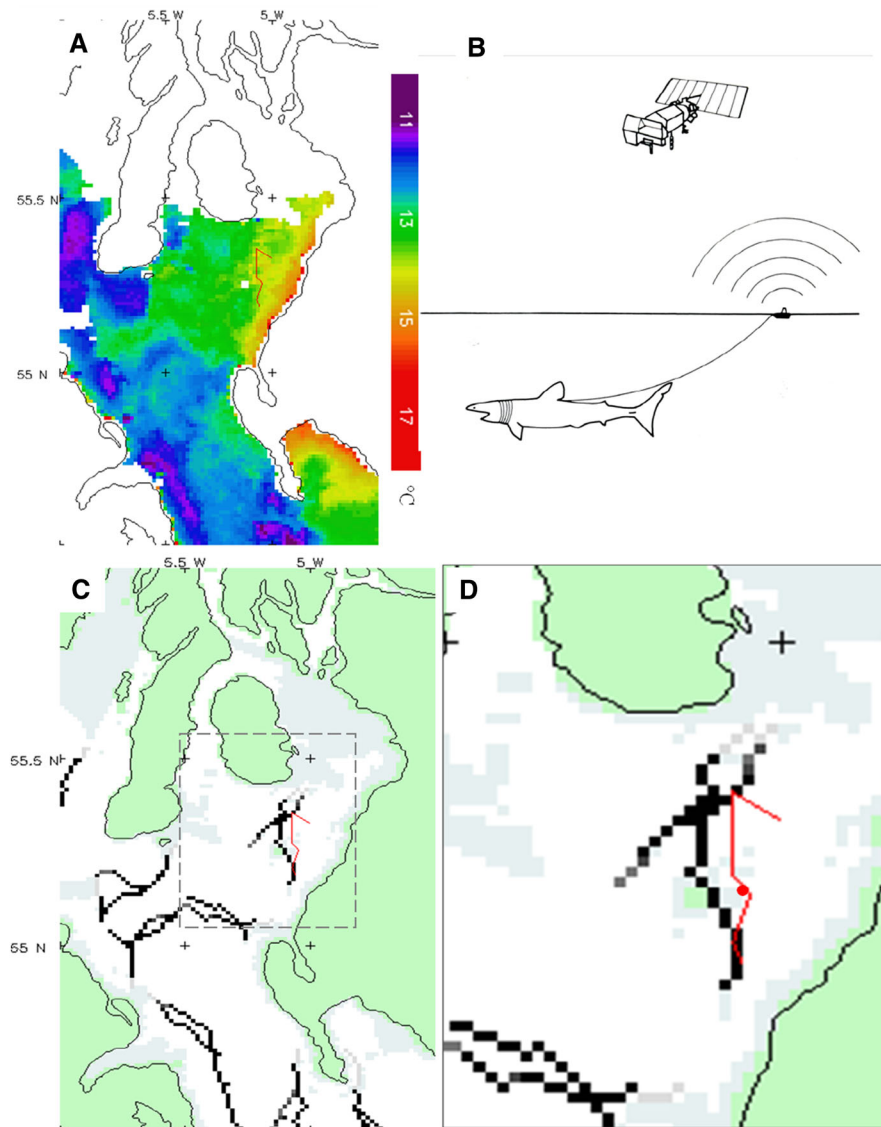


Figure 8

Tracking of a basking shark, *Cetorhinus maximus* with simultaneous remote sensing (PRIEDE 1984; PRIEDE and MILLER 2009). **a** AVHRR SST (sea-surface temperature) scene acquired on 06 July 1982 at 1429 UTC off the west coast of Scotland. The *red line* shows the track of the basking shark. **b** Configuration of the shark with the ARGOS transmitter attached via a tether. **c** Composite front map derived from AVHRR SST data between 03 and 09 July 1982. The *red line* shows the satellite-tagged basking shark track during 06 July in the Firth of Clyde. *Grey areas* were covered by cloud during the entire 7 days. **d** Enlargement of Firth of Clyde region, with *red circle* indicating the shark location coincident with the AVHRR overpass at 1429 UTC

offshore. SIMS *et al.* (2006) have demonstrated that basking sharks, which feed on plankton, consistently occur in areas where fronts are most persistent (SIMS and QUAYLE 1998) reflecting the high productivity in such areas and increased probability of finding food. CHARRASSIN *et al.* (2008) used instrument-equipped southern elephant seals as platforms to investigate the

structure of fronts and processes of sea-ice formation in high latitude waters of the southern ocean, which was otherwise difficult to access by conventional methods.

A most remarkable study using animal tracking techniques has been TOPP (Tagging of Pacific Predators, <http://www.topp.org>) which has tracked 1,791

individual animals from 23 species, totalling 265,386 animal tracking days ranging throughout the Pacific Ocean. With such an extensive database, BLOCK *et al.* (2011) were able to show that the California Current large marine ecosystem (approximately equivalent to Longhurst's CALC, (Table 2; Fig. 6) is an important habitat for Pacific bluefin tuna *Thunnus orientalis*, yellowfin tuna *Thunnus albacores*, albacore *Thunnus alalunga*, shortfin Mako shark *Isurus oxyrinchus*, white shark *Carcharodon carcharias*, salmon shark *Lamna ditropis*, blue shark *Prionace glauca*, common thresher shark *Alopias vulpinus*, blue whale *Balaenoptera musculus*, northern elephant seal *Mirounga angustirostris*, California sea lion *Zalophus californianus*, Laysan albatross *Phoebastria immutabilis*, black-footed albatross *Phoebastria nigripes*, sooty shearwater *Puffinus griseus*, leatherback turtle *Dermochelys coriacea* and loggerhead turtle *Caretta caretta*. Several species that range widely across the Pacific Ocean made repeat visits to the CALC area of high productivity as part of their migration pattern. Defining zoogeographic areas therefore is not simply a matter of identifying species presence or absence; highly mobile species utilise different biomes in complex ways that can only be revealed by the global tracking capabilities offered by satellite-based systems. Whilst the results of satellite tracking have received widespread attention with real-time cartographic display of tracks on the program website, the technique has limitations. Firstly, the method is only applicable to animals large enough to carry the necessary transmitter package, including batteries. This confines the research to apex predators such as sharks and tunas and only the adults can be tracked. The life cycle of sea turtles involves remarkable migrations by adults, which have been tracked using satellite transmitters (HAYS *et al.* 1991) but such technology cannot be applied to the tiny hatchlings that undertake equally interesting migrations (HAYS 2008). Most marine animals are <0.5 kg in body weight and cannot be tracked by satellite since they cannot carry the weight of the necessary transmitter package. Secondly, satellite tracking can only work for animals that appear on the surface of the sea at regular intervals. For air-breathing species such as dolphins, whales or turtles this is clearly essential and tracking can be achieved. However, to obtain a reliable

Doppler location, as used by the ARGOS system, several uplinks to the satellite are necessary during a single orbit overpass. The mean surfacing time for a breath by the pan-tropical spotted dolphin (*Stenella attenuata*) is just over one second, barely sufficient time to transmit a single uplink message to the satellite (PRIEDE 1983). To obtain a good location, therefore, the dolphin must surface several times during the ca. 10 min of orbital overpass period when the satellite is at optimal elevation above the horizon. For most marine animals good quality locations are obtained on a small percentage of satellite overpasses, a problem exacerbated in tropical regions by the low frequency of overpasses owing to the polar orientation of the orbit of the satellites. These limitations have been overcome by logging environmental data such as dive depth and geo-location data that are inserted into the uplink messages, enhancing the information obtained through the sporadic tracking system (BLOCK *et al.* 2011; HAYS 2008). The argument has been applied that top predators can be used as a bellwether for environmental change; by monitoring the top predators it is possible to define the health of the ecosystem (BOYD *et al.* 2006) just as in ancient times shepherds attached a bell to a single animal, which enabled them to monitor the entire herd of sheep.

For the majority of life in the ocean interior, satellite tracking and remote sensing has limited applications. However life in the deep sea is dependent on export flux from the surface (SMITH *et al.* 2009; REX and ETTER 2010) and satellite-derived patterns of surface chlorophyll from OCTS (Ocean Color and Temperature Scanner), SeaWiFS, Terra-MODIS (Moderate Resolution Imaging Spectroradiometer) and Aqua-MODIS have been used to predict food supply to depths over 4,000 m (SMITH *et al.* 2006) The implications of this prediction from satellite data are vividly demonstrated by the discovery of two new species of torquaratorid acorn worms (Hemichordata, Enteropneusta) at 2,500-m depths in the middle of the Atlantic Ocean (PRIEDE *et al.* 2012) The more robust *Tergivelum cinnabarium* was most abundant at 54°N, north of the sub-polar front, whereas the wide-lipped *Yoda purpurata* occurred mainly south of the front. Despite their remoteness from the surface, these animals are

apparently adapted to the differences in export flux of detritus from the surface upon which they are depend for their food.

Major biogeographic problems remain in understanding “what lives where?” Very interesting progress has been made in using distinctive optical signatures of different phytoplankton communities to discriminate; plankton size classes, phytoplankton taxonomic groups or phytoplankton functional groups from satellite remote sensing of ocean colour (AIKEN *et al.* 2007; BREWIN *et al.* 2010; MOISAN *et al.* 2012). SATHYENDRANATH *et al.* (2004) demonstrated discrimination of diatoms from other phytoplankton arguably direct sensing of biogeography from space. Attention has also shifted towards the role of the oceans in global biogeochemical cycles (SARMIENTO and GRUBER 2006; BALLANTYNE *et al.* 2012). It is generally accepted that the oceans play a major role in draw-down of CO₂ from the atmosphere (SABINE *et al.* 2004) and much of that CO₂ is taken up and fixed by photosynthesis in the surface layers and exported to the abyss in the form of organic matter (SMITH *et al.* 2009). Some however is retained in the upper ocean as Dissolved Organic Carbon (CARLSON *et al.* 1994). Ultimately, an understanding of the draw-down of CO₂, its fixation, and the export of resultant organic carbon into the ocean interior will require knowledge of taxonomy and biogeography of the species comprising the “biological pump” mediating these processes.

5. Conclusions

PRIEDE (1983) wrote that “*Use of satellite based instruments has not achieved wide acceptance amongst marine biologists*”. At the time, the technologies were in their infancy and 30 years later there is no doubt that satellite-based techniques have revolutionised marine science. Satellite tracking of animals and remote sensing of ocean colour are now routine “tools of the trade” in marine biology. A sceptic might argue that the recognition of Polar, Trade Wind and Westerly Biomes represent little advance over the synthesis achieved at the time of MAURY (1855) over 150 years ago. In some senses, our understanding of the oceans has been a gradual

process with satellites simply adding further increments to that knowledge. However, the daily global real-time coverage provided by satellites and the volume of data compared with the hand-written log books of nineteenth century ships’ captains mean that our capacity to document the biogeography of the oceans is unprecedented and furthermore the science is well-placed to assess anticipated global changes in environment (SMITH *et al.* 2006).

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