From OCEANIC SOUND SCATTERING PREDICTION
Edited by Neil R. Andersen, and Bernard J. Zahuranec
[Plenum Press, 1977]

THE CYCLING OF LABILE ORGANIC COMPOUNDS: STEROLS IN THE NORTH ATLANTIC OCEAN

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ABSTRACT

Seawater samples collected from the continental shelf and slope waters of the western North Atlantic Ocean and Sargasso Sea have been analyzed for a class of biogenic compounds, the sterols. The sterol concentrations found ranged from 0.1 to 1.3 µg/l seawater. Cholesterol is the major free and esterified sterol in both the surface and deep water. β-Sitosterol, fucosterol, brassicasterol, 22-dehydrocholesterol, campesterol, 24-methylenecholesterol, norcholestadienol and stigmasterol are found in lower concentrations at the surface and in the deep sea. Several sterols, e.g. brassicasterol, appear to be produced and consumed in the upper 1000 m of the water column, whereas few sterols, e.g. cholesterol, were found in the entire water column and may be examples of more resistant organic compounds.

Several mechanisms can be postulated for the injection of sterols into the deep sea. Vertical fluxes of organic particles from the surface appear to deliver sterols into the mid-depth waters of the Sargasso Sea. However, some other process(es), e.g. physical transport (viz. horizontal and vertical advection and diffusion), resuspension of sediments, or in situ deep water biological production and consumption, is controlling deep water sterol distributions. Detailed profiles of ancillary data such as particulate organic carbon, hydrographic and total particulate matter collected at the same station are necessary to complement detailed profiles of specific organic compounds in order to discern the transport mechanisms of these biochemicals to the deep sea.

INTRODUCTION

The cycling of organic matter in the sea has received a great deal of attention in recent years. For the most part, this has involved the collection of extensive data concerned with the properties of mixtures of organic comounds such as particulate and dissolved organic carbon (POC and DOC) (*Sharp*, 1973; *Menzel*, 1974), delta C^{13} (*Williams and Gordon*, 1970), spectral parameters (*Mattson et al.*, 1974) and biological oxygen demand (*Zsolnay*, 1975). This "bulk" approach, however, describes the integrated result of several simultaneously occurring processes affecting the specific classes of organic compounds in the organic matter pool. It would, therefore, be fruitful to study the cycling of individual, specific classes of organic compounds in order to use them as tracers in separating the myriad of mechanisms and processes governing the cycling of bulk organic matter. In addition, it is the labile organic compounds, rather than the more resistant organic matter, which take part in the nutritional and hormonal processes of deep sea biota. Hence, knowledge of the origin, transport, and sinks of labile organic compounds is most important to our understanding of deep sea biological activity.

There is, however, very little information on the origin, distribution and fate of organic compounds in the sea. Even less is known about their geographical and temporal variations. Data concerning the rates and mechanisms of organic chemical processes in the oceans are practically non-existent and the mechanisms that govern the transport of organic compounds to the deep sea are not clear. Two of the major reasons for this paucity of information are the complexity of the analytical techniques required for the quantification of organic compounds from seawater and the contamination problems associated with these analyses.

The chemical structures of only 10 to 20% of the dissolved organic matter in seawater have been elucidated (*Hood*, 1971; *Riley and Chester*, 1971; *Wagner*, 1969; *Wangersky*, 1972; *Williams*, 1971). This fraction consists of amino acids, sugars, urea, hydrocarbons, organic pigments and acids, and fatty acids and alcohols. Recently, another class of marine biochemicals, the sterols, has been studied (*Gagosian*, 1975a; *Gagosian*, 1976). The sterols are among the most important hormone regulators of growth, respiration and reproduction in organisms. Cholesterol and related steroid alcohols are not only the immediate biosynthetic precursors for all steroidal hormones, but they also have hormonal activity themselves (*Kanazawa and Teshima*, 1971a). These steroidal alcohols, the sterols, are of special interest from a geochemical point of view. Their chemical stability and structural diversity, along with their inherent optical activity, allow them to be used as indicators of biological activity in the oceans.

In seawater, sterols act as good tracers of biogenic material in the complex mixture of dissolved and particulate matter. After deposition to the sediments, sterols should become useful indicators of geochemical processes in recent sediments. Sterols may provide infor-

mation on the marine or terrestrial, plant or animal origin of sedimentary organic matter.

It is known that most marine invertebrates are unable to biosynthesize sterols (*Zandee*, 1964, 1967). Therefore, they must obtain them from exogenous sources, such as by adsorption or filtration from seawater. Hence, the presence of dissolved sterols in seawater is of interest as they have a role in the food chain, particularly with regard to zooplankton. The sterols of particulate matter may be of equal importance and they may be utilized as a dietary supplement for the larvae of marine animals.

In this manuscript the results of three cruises concerned with the sterol concentrations and individual sterol distributions in the North Atlantic Ocean are reported. From the vertical profiles of these compounds, along with POC, hydrographic and total particulate matter data, an attempt to understand sterol distributions in the ocean and the transport mechanisms governing their movement into the deep sea was undertaken.

Sampling and Analyses

In 1973 and 1974 Cruise 33 of R/V Knorr and Cruises 82 and 85 of the R/V Atlantis II were conducted in the Sargasso Sea and slope waters of the North Atlantic Ocean. Five stations of large volume samples were occupied, the last being the most detailed. The large volume samples for sterols and particulate organic carbon (POC) were obtained with 60 liter aluminum Bodman bottles (*Bodman et al.*, 1961) as previously described (*Gagosian*, 1975a). At each location a complete hydrographic station was simultaneously made, using Teflon-lined Nansen bottles.

Sterols were extracted from seawater and analyzed by the methods previously described (*Gagosian*, 1975a). Briefly, 20 liter samples were transferred from the Bodman bottles to thoroughly precleaned five gallon glass carboys. The samples were then doubly extracted in 5 liter glass separatory funnels with hexane. The hexane extracts were placed in precleaned pint bottles with Teflon caps and stored in a freezer for shore-based analysis. Blanks were run for the entire process. After returning to shore the hexane extracts were concentrated on a rotary evaporator, lyophilized, and derivatized to make the trimethylsilyl ether of the alcohol functional group. Quantification and structural elucidation were then determined by gas chromatography, and gas chromatography-mass spectrometry. The lower limit of sterol detectability is 1 ng of each sterol/l seawater. The reproducibility of replicate samples is ± 5%; sample variability is ± 15% for samples taken at the same location and depth in the Sargasso Sea. The blank value for sterols is 30 ng/l seawater.

Samples for POC were analyzed as described by *Gagosian* (*Gagosian*, 1976). Briefly, the seawater samples (4 liter surface water and 10 liter deep water) were transferred to a 12 liter fiber glass container and pressurized to less than 5 lbs. N_2. The samples were then

filtered through Gelman Type A (1-2 μ pore size) glass fiber filters which had been precombusted at 450°C for 24 hours. After filtration, the filters were carefully separated, dried, and stored in a freezer for shore-based analysis. After returning to shore, the filters were again dried, and total organic C was determined by dry combustion on a Perkin Elmer CHN analyzer. The reproducibility for the combined sampling and analysis, as determined by replicate analyses is ± 7% and the blank for entire procedure is 2.5 μg C/l for deep water and 5 μg C/l for surface water. Total particulate matter samples were taken from 30 liter PVC Niskin bottles and analyzed by Dr. D. W. Spencer of this institution. DOC analyses were not made due to controversy on the validity of DOC determination methods (*Menzel and Vaccaro*, 1964; *Sharp*, 1973).

RESULTS AND DISCUSSION

Sterol Sources in Seawater

There are several sources of sterols in the surface waters of the ocean. The majority of marine sterols contain 27-29 carbon atoms, with the C_{29} sterols being predominant. However, recent discoveries of a norcholesterol and of gorgosterol and its analogs have increased the range of marine sterols from C_{25} to C_{30}. It should be noted that the variation in number of carbon atoms occurs almost exclusively on the side chain, mainly at C-24 (see Figure 1, structure 2). Other structural diversity that exists is found almost entirely in the side chain, except for the saturation of ring B to form the reduced sterols, the stanols (Figure 1, structure 4), and the dehydration and the saturation of rings A and B to form the cycloalkane steranes.

General reviews have recently appeared on sterols in marine organisms (*Scheuer*, 1973) and sterols of marine invertebrates and plants (*Austin*, 1970). More specific reviews have been prepared on sterols in mollusca (*Idler and Wiseman*, 1971a), echinoderms (*Goad et al.*, 1972), and crustacea (*Idler and Wiseman*, 1971b). The distribution and function of sterols in algae have been reviewed by *Heftmann* (1971) and *Patterson* (1971). Sterols in fungi have been reviewed by *Weete* (1973).

From these reviews, we find a large diversity of structures and a wide distribution of sterols in a concentration range of 0.01% to 2% for marine invertebrates, and 0.005% to 0.5% for marine plants. Cholesterol was found to be the most abundant sterol in the advanced invertebrates, whereas the more primitive invertebrates have much more diversified sterol compositions (*Austin*, 1970; *Gagosian*, 1975b; *Idler and Wiseman*, 1971b). The primary sterol found in brown algae (*Phaephyta*) is fucosterol (*Safe et al.*, 1974; *Smith et al.*, 1973). Red algae (*Rhodophyta*) contain mainly cholesterol and desmosterol with a few exceptions. Green algae (*Chlorophyta*) have a very complex

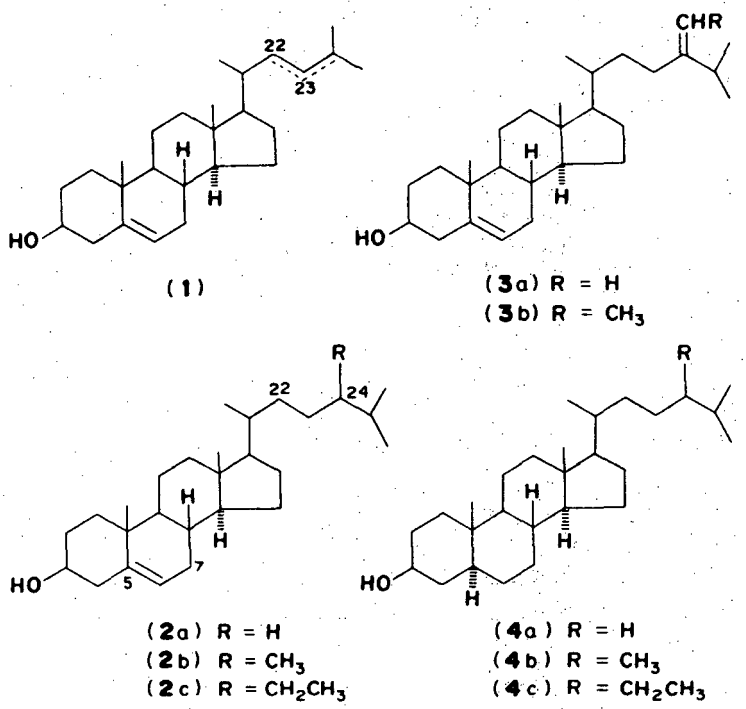

Fig. 1. Structures of sterols isolated from seawater of the North Atlantic Ocean.

sterol composition of some twenty to twenty-five compounds. Two species of marine diatoms, *Cyclotella nana*, and *Nitzschia closterium*, were found to contain only brassicasterol (*Kanazawa et al.*, 1971).

A few species of bacteria (*Schubert et al.*, 1968) and blue green algae (*DeSouza and Nes*, 1968; *Reitz and Hamilton*, 1968; *Teshima and Kanazawa*, 1972) contain sterols, but at very low concentrations. Several species of bacteria have no sterols at all (*Schubert et al.*, 1968). The apparent lack of steroidal compounds in bacteria potentially makes this class of compounds particularly useful as a tracer of organic processes in the sea since other organic compounds such as amino acids, sugars and fatty acids are present in bacteria. Marine yeasts contain from .01% to 0.1% sterols, ergosterol and campesterol being the major components (*Teshima and Kanazawa*, 1971). *Boutry* (1967, 1970) has recently calculated a concentration of 0.4% sterols in phytoplankton collected from the Mediterranean Sea, with cholesterol and 24-methylenecholesterol being the major components, and campesterol, stigmasterol and β-sitosterol concentrations ranging from 1-5% of the total. Cholesterol was found to be the major component of the sterol mixture in

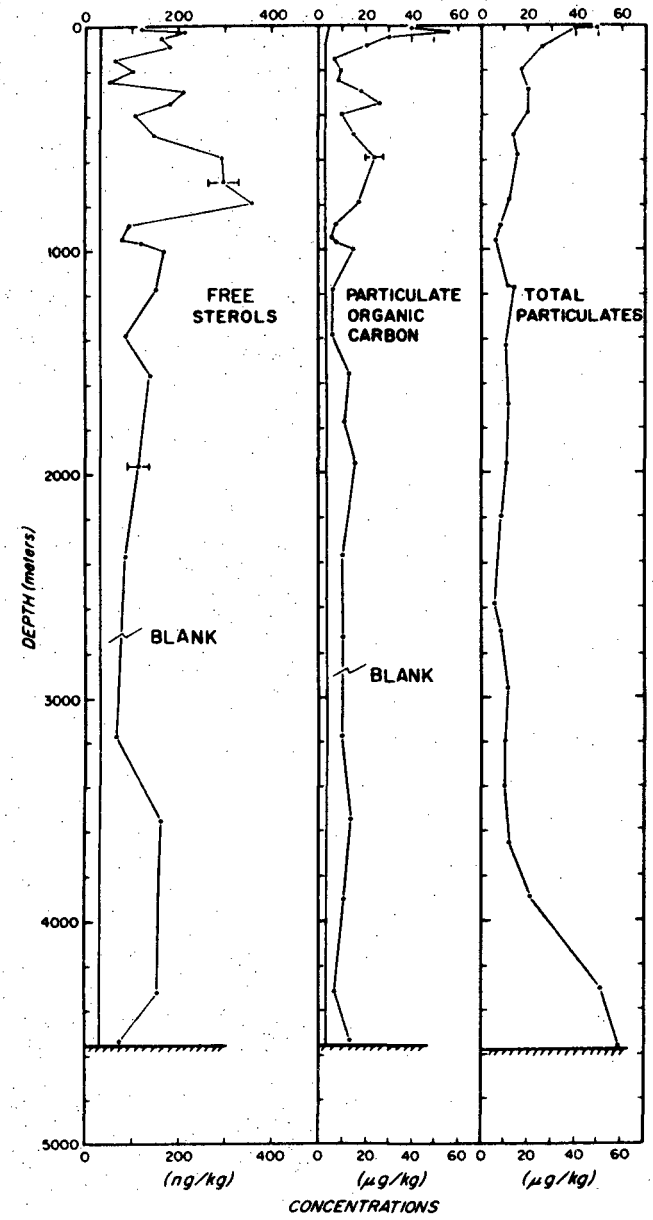

Fig. 2. Total free sterol, particulate organic carbon, and total particulate matter concentrations as a function of depth from 33°40.6'N; 57°36.8'W - September, 1974. POC and sterol samples were taken from the same sampler, whereas those for total particulate matter were taken from Niskin bottles on the same cast. Therefore, POC values found to be greater than total particulate matter at the same depth probably reflect sample variability.

zooplankton collected from the Mediterranean Sea. β-Sitosterol is a common terrestrial plant sterol isolated in high concentration, and may enter the marine environment through river runoff or aeolian transport on particulates. This sterol has also been found in coastal grasses in the Gulf of Mexico (*Attaway et al.*, 1971).

Sterol Distributions in Seawater

During the past two years we have analyzed seawater samples collected on two cruises concerned with the sterol concentrations and individual sterol distributions in both the surface and deep waters of the continental shelf and slope waters of the North Atlantic Ocean and the Sargasso Sea (*Gagosian*, 1975a). In addition, we have analyzed samples and constructed detailed vertical profiles of free sterols (extractable into organic solvent), POC and total particulate matter at a station in the Sargasso Sea (33°40.6'N; 57°36.8'W) (Figure 2). The sterol profiles constructed from this data are some of the most detailed profiles reported for any single class of biochemicals in seawater. Hydrographic data for this station is presented elsewhere (*Gagosian*, 1976).

Assigned structures of the sterols isolated are shown in Figure 1. Table 1 lists the molecular formulas and common names of these compounds. The peak numbers refer to the peaks in the gas chromatograms (*Gagosian*, 1975a).

Sterol Concentrations in the Water Column. The sterol concentrations of the deep water samples are listed in Table 2, with corresponding station numbers, potential temperatures, salinities, and depths. From the temperature-salinity data of Table 2, one concludes that sample K-33-II-1 contained a mixture of overlying water, Labrador Sea water, and possibly some Mediterranean Sea water (*Spencer*, 1972; *Worthington and Wright*, 1970). K-33-II-2, sampled at 3095 m, contained North Atlantic Deep water composed of Iceland-Scotland Overflow and Denmark Strait Overflow water. K-33-II-3 and K-33-I-8 samples collected from 4630 m and 4142 m respectively, contained Antarctic Bottom water mixed with North Atlantic Deep water (*Spencer*, 1972).

Samples collected in the Sargasso Sea in September, 1973, at Stations 6 and 7 exhibit bottom water sterol concentrations approximately equal to sterol concentrations of the surface samples (Table 2). However, deep water samples collected in February from the edge and rise of the continental shelf south of George's Banks at Stations C and D exhibit lower sterol concentrations than those found in the surface waters of these stations. Sample K-33-I-6 (Station 6), taken at 80 m in the summer thermocline of the Sargasso Sea, is almost a factor of two higher in both free and total sterol concentrations than the surface and deep water samples collected at this station. Also, at Station 6 particulate organic carbon (POC) values from just below the summer thermocline (80-90 m) are higher than their surface water values. Thus, a correlation of sterol concen-

TABLE 1. Sterols Isolated and Identified from North Atlantic Ocean Samples by Gas Chromatography-Mass Spectrometry

Peak No.	Formula	Assignment	Structure (Figure 1)
1	$C_{26}H_{42}O$	Norcholestadienol	1Δ^{22} or Δ^{23}
2	$C_{27}H_{44}O$	22-Dehydrocholesterol	2a Δ^{22}
3	$C_{27}H_{46}O$	Cholesterol	2a
4	$C_{28}H_{46}O$	Brassicasterol	2b Δ^{22}
5[1]	$C_{28}H_{44}O$	Ergosterol	2b Δ^{7}, Δ^{22}
6 (a)	$C_{28}H_{48}O$	Campesterol	2b
(b)	$C_{28}H_{46}O$	24-Methylenecholesterol	3a
7	$C_{29}H_{48}O$	Stigmasterol	2c Δ^{22}
8 (a)	$C_{29}H_{50}O$	β-Sitosterol	2c
(b)	$C_{29}H_{48}O$	Fucosterol	3b

[1] Quantities isolated were too small for absolute structural assignment.

tration with POC does exist for these samples from the euphotic zone. This correlation can be seen further from the total free sterol (extractable into organic solvents and not saponified) and POC concentrations plotted as a function of depth in Figure 2. The blank values for sterols and POC have not been subtracted from the data presented on the profiles, but are shown on the profiles. In the upper 1000 m, variations in sterol concentration correlate closely with POC and considerably less, if at all, with total particulate matter. The sterol water samples were unfiltered. As a

TABLE 2. Sterol Concentrations in Subsurface Seawater from the North Atlantic Ocean (in ng/l)

Sample No.	Depth (m)	Potential Temperature (°C)	Salinity (°/oo)	Total Sterols Free	Total Sterols Free and Esterified
Location - Station No. 7 (27°50'N, 67°26'W) 4938 m water column					
K-33-II-4	7	27.40	36.503	200	380
-1	993	6.47	35.214	120	330
-2	3095	2.50	34.944	170	320
-3	4630	1.80	34.891	230	450
Location - Station No. 6 (32°20'N, 63°00'W) 4380 m water column					
K-33-I-5	7	27.40	36.554	390	610
-6	80	20.38	36.495	700	1350
-7	702	12.74	35.870	260	340
-8	4142	1.86	34.887	360	710
Location - Station D (39°58'N, 67°00'W) 3050 m water column					
AII-81-5	10	10.15	34.116	660	710
-6	110	14.33	35.448	390	610
-7	1989	3.36	34.964	340	-
Location - Station C (40°00'N, 69°02'W) 1150 m water column					
AII-81-4	8	11.13	34.196	710	900
-3	1100	4.88	34.991	390	570

result, this good correlation suggests that most sterols in the upper 1000 m are associated with POC. However, this correlation of sterols with POC is not as pronounced in the deep water, suggesting some other process may be controlling the sterol distributions. At 3600 m an increase in total sterol concentration is observed. This increase is very slight for POC which is roughly constant from 1200 m to the bottom at about 6 µg/l.

The lack of comparable data from other stations makes it difficult to draw any conclusions from a single vertical profile. However, several features of the sterol profile (Figure 2) are worthy of mention. The maxima at 40-50 m for both sterols and POC may be due to either *in situ* biological productivity or a change in the density gradient at the bottom of the summer thermocline. Sargasso Sea 18°C water is between 250-350 m at these stations. Therefore, the maxima at 300 m in the vertical profile for both sterols and POC may be due to this advective feature. The oxygen minimum and phosphate and nitrate maxima occur at 750 m at this station where a large sterol maximum occurs. Remineralization of biogenic detritus releasing several bound organic compounds which would not generally be extractable from seawater by organic solvents (for example, due to entrapment in carbonate particles) may be occurring, thus yielding higher concentrations of soluble sterols. However, *in situ* production or advective processes cannot be ruled out.

A minimum in the profile occurs at 950 m. This is where the influence of Mediterranean Sea water is the the strongest. One would not expect to see this small input (approximately 2%) reflected in sterol concentrations even if Mediterranean Sea water sterol concentrations were zero because the sterol sample analytical uncertainty is $\pm$ 15%. The reason for this 950 m minimum is therefore unknown. However, it is interesting to note that the minimum is also present in the POC and total particulate matter profiles. The increase of sterols in the deep water at 3600 m and 4350 m does not appear to correlate linearly with POC. Since the appearance of the nepheloid layer in this region of the North Atlantic Ocean occurs at this depth (*Biscaye and Eittreim*, 1974), correlation of sterol concentrations with the resuspension of particles from bottom sediments is tempting. Advective and diffusive processes from North Atlantic Ocean deep water and Antarctic Ocean bottom water may also be responsible for the deep sea sterol concentrations observed. Data concerning sterol concentrations in the dissolved and particulate fractions of seawater are necessary to further elucidate the processes outlined above.

Distribution of Individual Sterols. The distributions for the individual sterols are given in Table 3 and Figure 3. The percent compositions of each sterol in both the free and total (free + esterified) sterol fractions are listed in Table 3. Cholesterol and β-sitosterol are the most abundant free sterols in the deep water. The norcholestadienol and 22-dehydrocholesterol are next in order of abundance while stigmasterol, campesterol, 22-methylenecholesterol, and ergosterol have lower percentages. Brassicasterol, not only has the lowest concentration of all the sterols, but decreases to a lower percent composition with depth in the water column at all four stations (Table 3) and in the detailed profile (Figure 3). As mentioned earlier, brassicasterol is an algal sterol. Hence, its low concentration in the deep water is not surprising. The large maximum in brassicasterol concentration at 600-800 m may be due to remineral-

TABLE 3. Sterol Distributions in Subsurface Seawater from the North Atlantic Ocean

Sample Number	Depth (m)	% Composition — Sterols: Norcholesta-dienol	22-Dehydro-cholesterol	Chole-sterol	Brassi-casterol	Ergo-sterol	Campe-sterol	Stigma-sterol	β-Sito-sterol
Location — Station No. 7 — 4938 m Water Column									
Free Sterols									
K-33-II-4	7	9	13	23	12	—	—	8	31
-1	993	11	—	43	—	—	—	—	47
-2	3095	9	—	48	—	—	—	4	39
-3	4630	9	7	24	—	5	—	4	37
Total Sterols[1]									
K-33-II-4	7	5	8	56	10	—	—	4	17
-1	993	4	—	62	—	—	—	6	28
-2	3095	2	—	75	—	—	—	2	21
-3	4630	10	4	46	—	3	—	3	25
Location — Station No. 6 — 4380 m Water Column									
Free Sterols									
K-33-I-5	7	3	8	39	15	—	1	6	28
-6	80[2]	10	9	30	6	5	3	3	22
-7	702	5	3	45	—	3	5	5	24
-8	4142[2]	6	—	54	—	2	2	4	21
Total Sterols[1]									
K-33-I-5	7	2	5	50	17	—	2	6	19
-6	80[3]	5	6	50	8	3	2	5	14
-7	702	2	2	54	3	3	3	4	19
-8	4142[3]	9	6	50	2	1	1	5	19
Location — Station D — 3050 m Water Column									
Free Sterols									
AII-81-5	10	7	12	14	17	—	8	4	29
-6	110	12	11	21	8	3	3	5	37
-7	1989	17	11	22	—	3	3	6	39
Total Sterols[1]									
AII-81-5	10	6	10	32	10	—	6	4	25
-6	110	7	7	49	6	2	2	7	20
Location — Station C — 1150 m Water Column									
Free Sterols									
AII-81-4	8[2]	10	11	26	13	—	7	4	22
-3	1100	14	9	23	1	3	2	5	35
Total Sterols[1]									
AII-81-4	8[3]	6	10	24	10	—	7	5	26
-3	1100	5	9	40	2	2	4	5	25

[1]Total Sterol Percentage = Free and Esterified Sterols.
[2]A Sterol Peak at 2.55 Retention Time Representing 3% was Present.
[3]A Sterol Peak at 2.55 Retention Time Representing 2% was Present.

ization of sterols bound to organic matter derived from algae, or to physical mixing processes, the same explanations given for the total free sterol maximum at 600–800 m. The fact that brassicasterol is not found deeper than 800 m leads one to believe that this is a

fairly labile sterol and is recycled in the top 1000 m of the ocean (Figure 3).

From the gas chromatograms of samples analyzed from Station 6 at 7 m, 80 m, 702 m and 4142 m (*Gagosian*, 1975a), Table 3 and Figure 3, one concludes that below 800 m all the sterol concentrations decrease with increasing depth in the water column except for cholesterol. The reason for the sharp decrease for cholesterol 10 m above the sediment-water interface is now known. Bacteria are known to reduce cholesterol (mw 386) to cholestanol (mw 388) (Figure 1, structure 4a) (*Eyssen*, 1974). Surface sediments in this study area contain many of these reduced sterols (*Gagosian*, unpublished data). It is possible, therefore, that resuspended sediment just above the bottom provides the sites for this biochemical reduction of sterols, and this is reflected by the low cholesterol concentration 10 m above the bottom. Alternatively, these deep water distributions may be a reflection of the surface sterol production at the original site of deep water formation. On the other hand, the distributional differences of individual sterols may be due to the decomposition or structural rearrangement of sterols by organisms during transport to the deep sea. In the euphotic zone phytoplankton produce several C-27, C-28 and C-29 sterols. The organisms living in the deeper water are cholesterol producers. They have the capability of transforming C-28 and C-29 sterols from phytoplankton through dealkylation processes into the C-27 sterol, cholesterol (*Teshima*, 1972). One or more of

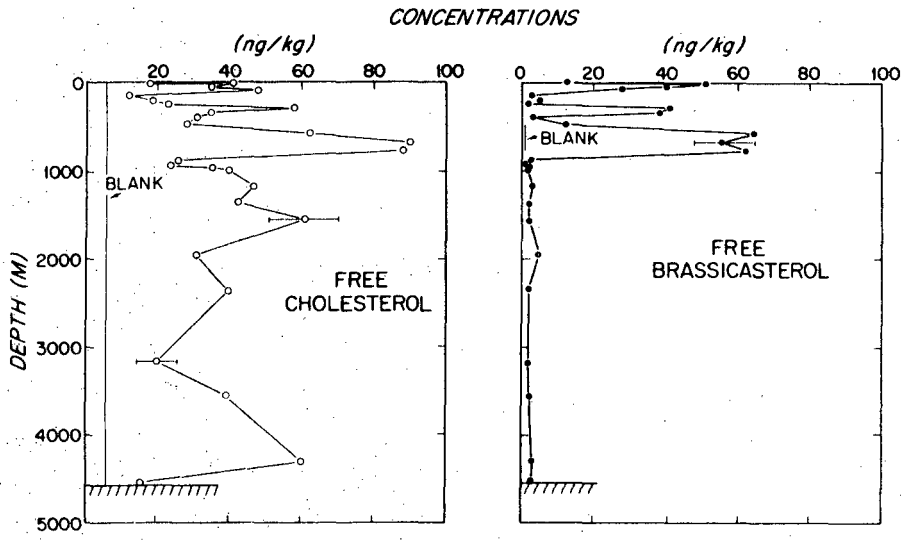

Fig. 3. The individual sterol concentrations of cholesterol and brassicasterol, as a function of depth from 33°40.6'N; 57°36.8'W.

the processes outlined above may be responsible for deep water sterol distributions.

Sterol Esters. By comparing the free and total (free and esterified) sterol percentages for each sterol peak in each sample in Table 3, it is evident that the only sterol percentages which are significantly higher for the total sterols are those of cholesterol (i.e., the ester fraction is made up almost exclusively of cholesterol esters). In the deep water samples cholesterol (free and esterified) is approximately half of the total sterol mixture. For the surface water samples, cholesterol (free and esterified) is from 30 to 40% of the total sterol fraction.

In both the surface and deep water samples, sterol esters comprise only about one-third of the total sterols. This observation is unexpected because plant and animal sterols are usually found in the esterified state with fatty acids or as sulfate conjugates. It is clear, then, that the residence times of sterol esters in the surface waters of the open ocean are quite low. Some esters, however, are not hydrolyzed, even by the time they are transported to the deep water. These compounds may be bound either on or in organic or inorganic detritus which protects the sterol esters from chemical or biochemical hydrolysis. The presence of sterol esters in the deep sea may be due not only to vertical transport on detritus, but also to *in situ* production. Sterol ester production in the deep sea should be considerably lower than in the highly productive euphotic zone. However, the hydrolysis rates of sterol esters in the deep sea may be considerably slower than those in the surface waters. If this is true, then the steady-state concentration of sterol esters in both the deep and surface waters could be approximately the same.

SUMMARY

We have observed from this work that:

(1) Detailed profiles of ancillary data such as POC, hydrographic, and total particulate matter collected at the same station are necessary to complement profiles of specific organic compounds in order to discern the transport mechanisms of these biochemicals to the deep sea.

(2) Free and esterified sterols are present in the Sargasso Sea and the continental shelf and slope water of the western North Atlantic Ocean in the 0.1 - 1.3 μg/l range.

(3) Cholesterol is the major free sterol in both the surface and deep water. β-Sitosterol, fucosterol, brassicasterol, 22-dehydrocholesterol, campesterol, 22-methylenecholesterol, norcholestadienol and stigmasterol are found in lower concentrations at the surface and in the deep sea.

(4) The major sterol esters found in both the surface and deep water are cholesterol esters with very low concentrations of other sterol esters.

(5) Several sterols (e.g., brassicasterol) appear to be produced and consumed in the upper 1000 m of the water column, whereas few sterols (e.g., cholesterol) were found in the entire water column and may be examples of more resistant organic compounds.

Several mechanisms can be postulated for the injection of sterols into the deep sea. Vertical fluxes of organic particles from the surface appear to deliver sterols into the mid-depth waters of the Sargasso Sea. However, some other process(es) is controlling deep water distributions. Physical transport processes (viz. horizontal and vertical advection and diffusion) may be responsible for control of these deep water concentrations. In addition, *in situ* deep water biological production and consumption cannot be ruled out and inputs from sediment resuspension must be considered.

Further work concerning more detailed profiles of sterols and comparisons with nutrients, primary productivity, hydrographic and POC data along with samples from varying oceanic environments (e.g., upwelling areas and anoxic basins) are needed in order to further evaluate the cycling of these most characteristic biogenic substances.

ACKNOWLEDGEMENTS

This research was supported by the Office of Sea Grant of the Department of Commerce (22-2000) and the National Science Foundation (GA-44224). Ms. Gale Nigrelli was responsible for a large amount of the extraction and analytical work described here. This paper is Woods Hole Oceanographic Institution Contribution No. 3667.

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