# SCIENCE

### Natural Marine Oil Seepage

Petroleum seepage into the marine environment is on the order of  $0.6 \times 10^6$  metric tons per year.

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A portion of the oil now present in the world's oceans results from the direct discharge of submarine seeps (1) into the water. Proper assessment of the present "hydrocarbon load" carried by the oceans, that is, the proportion contributed by natural sources and by man, requires a reliable estimate of the yearly worldwide seepage rate from marine seeps (2). Although only a very few marine oil seeps are presently known and located, all evidence suggests that, with further investigation, many more will be found. In view of the limited observations, only a few cursory estimates (3) of total worldwide annual marine seepage have been made; there appears to be no substantiation for any of these estimates. This article, which represents a first documented approach based on geologic considerations, presents an estimate of yearly oil input into the oceans from naturally occurring marine seepage.

A geologic model based on structural styles, recent earthquake activity, and sediment thicknesses was used to classify the continental margins into areas of high, moderate, and low seepage potential. Flow rate data for each of the three type potential areas were fitted to a log-normal probability distribution [the assumption was made that the logarithm of the flow rate would follow the normal, or Gaussian, density function,  $\sim e^{-x^2}$ ; the problem then became to find the parameters of

that function (4)], and seepage volumes were determined.

The probable range of seepage into the marine environment is  $0.2 \times 10^6$  to  $6.0 \times 10^6$  metric tons per year. Within this range the best estimate for present marine seepage worldwide is on the order of  $0.6 \times 10^6$  metric tons per year. On the basis of this estimate, areas of high seepage potential contribute about 45 percent of the worldwide seepage. In the Pacific Ocean, high seep potential areas are by far the major contributors. In the Atlantic and Indian oceans, moderate seep potential areas are most significant. The circum-Pacific area is the area of greatest seepage; it is estimated to contribute about 40 percent of the world's total.

#### **Seep Occurrences**

Natural seepages have been documented throughout written history, as evidenced by biblical references, the works of Herodotus (5), and the writings of Marco Polo (6). In the early days of petroleum exploration land seeps were widely used as an exploration tool, which led to an active search for them as well as an accurate description of their locations and even limited descriptions of their characteristics. However, accounts of marine seep occurrences are scarce. A preliminary literature survey revealed 190 reported marine seeps worldwide (7). These occurrences are plotted in Fig. 1.

The limited record of marine seeps is no doubt a reflection of the difficulty of observation in the marine environment as well as a function of the less extensive exploration of offshore areas by comparison with onshore areas. The residual evidence of intermittent seepages in the form of tar or asphaltic stains, so apparent on land, is hidden by water. Scuba divers have observed seeps off southern California that rarely break water. There some seeps form long stringers that trap sediments and sink to the sea floor as submarine mounds. Other seeps may form tar flows or mats on the ocean floor (8). In addition, the dispersing effect of the oceans makes both observation and location of marine seeps problematical.

Even in areas where marine seeps are known, it is expected that more detailed investigations will reveal a far greater number of seeps than have thus far been recorded. Recent experience off the coast of southern California shows that, prior to the detailed studies of Wilkinson (9), only a few marine seeps were reported, including those at Coal Oil Point and at Santa Monica Bay. When this area was examined in more detail, the number increased to 50 or 60 confirmed seeps.

Although there is evidence of substantial seepage volumes, few direct measurements of flow rates (barrels of oil per day per seep) have been made (10). Reported rates range from as much as 900 barrels per day at Coal Oil Point off southern California to a fraction of a barrel per day at a number of localities off the coast of western Canada and Alaska.

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The Coal Oil Point seep in California is generally considered an exceptionally large seep with a high flow rate. There is also evidence of large seeps in other areas of the world. Huge blocks of asphalt have been found floating on the Dead Sea; a block weighing "about 20 tons" was reported in 1958 (11). Asphalt Lake on Trinidad had a stream of asphalt, sediment, and water 15 to 18 feet (4.5 to 5.5 meters) deep that flowed continually to the sea before mining of the asphalt commenced (11). The Athabasca tar sands ( $800 \times$ 109 barrels) in Canada are the remains of a giant seep.

A study of land seeps is essential to determine marine seepage. Seismic data, drilling, and other geologic data have shown that similar geologic conditions exist on land and in the oceanic areas adjacent to the continents. As a result, natural seepages from both areas can be expected to behave in a similar manner and to be functions of the same geologic and geochemical parameters.

The locations and the number of seeps on land have been compiled from numerous sources and are also included in Fig. 1. Although the coverage is not complete, it indicates the broad geographic and geologic distribution of onshore oil seeps. In Fig. 1 "seepage areas" are generally shown because in a given locality many small seeps usually combine to produce a significant seepage. For example, Fig. 1 notes 64 "seeps" in the entire Tampico basin, Mexico, whereas DeGolyer (12) mapped and counted more than 6000 individual seepages in the Cerro Azul locality, which is only one small area within this basin. There are few or no data available from some large geographic areas because of political barriers (Russia and China) or because of climate or inaccessibility (Arctic and Antarctic regions, the Amazon basin in South America, parts of Africa, and most of Alaska and northern Canada). In addition, certain geologic provinces, such as shield areas (eastern Canada, western Australia, and eastern Brazil), do not contain oil seeps. It is clear, however, that there are areas with many seeps as well as areas where few if any seeps occur. These differences are dependent on geologic and geochemical conditions.

Although oil seeps occur almost exclusively in sedimentary rocks or in metamorphic or igneous rocks closely associated with sediments, they are found in a number of different geoTable 1. Geologic criteria for evaluating the seepage potential of offshore areas.

High potential for seepage

- (i) Strike-slip faulting associated with high incidence of earthquakes
- (ii) Tight compressive folding associated with high incidence of earthquakes
- (iii) Igneous activity
- (iv) Thick geochemically mature Tertiary sediments
- Moderate potential for seepage
  - (i) Strike-slip faulting associated with low incidence of earthquakes
  - (ii) Trench-associated margins with high incidence of deep earthquakes
  - (iii) Early active phase of pull-apart margins
  - (iv) Growth faulting associated with giant, river-fed submarine fans
  - (v) Diapiric or intrusive structures (shale, salt, or igneous rocks)\*
- Low potential for seepage
  - (i) Pull-apart margins of the Atlantic type
  - (ii) Little indication of recent structuring
  - (iii) Little or no earthquake activity
  - (iv) Older sediments or geochemically immature young sediments

\* A diapir is a dome or anticlinal fold, the underlying rocks of which have been ruptured by the squeezing out of the plastic core material. Diapirs in sedimentary strata usually contain cores of salt or shale; igneous intrusions may also show diapiric structure (27).

logic situations. Seeps may originate from the breaching or truncation of an oil reservoir (such as at Windy Point, Northwest Territories, Canada); from leakage along faults (Coal Oil Point, California); from fractures associated with diapirs or intrusions of shale (Trinidad), salt (Iran, Rumania), or igneous rocks (Tampico region, Mexico); or as direct emanations from prolific source rocks (numerous Monterey shale occurrences in California).

Seeps may originate from commercial or noncommercial oil reservoirs as well as from petroleum source rocks. As a result, all seepage areas are not necessarily commercial petroleum provinces or indicative of reservoired petroleum. For example, despite extensive seepage in the northern half of Cuba and on the Philippine Islands, little petroleum has been found to date (13). Link (14) considered one of the main seepage types to be "seeps of oil found associated with beds and formations in which the oil was formed." Under normal conditions these source rocks have no free oil. However, upon crushing or shattering by fracturing, faulting, or folding, petroliferous source rocks such as shales or limestones can liberate free oil that results in seeps. Even in known oil-producing basins some of the seepage from prolific source rocks such as Cretaceous La Luna shales and limestones in Venezuela and Colombia and Miocene Monterey shales in California is not associated with petroleum reservoirs (15).

Comparison of the onshore and offshore seep frequency data (Fig. 1) with the worldwide seismicity map (Fig. 2) indicates a strong correlation between areas of high seepage and areas of current tectonic activity and structuring. This association of seepage and structure is demonstrated by a comparison of adjacent parts of the Persian Gulf basin. The Zagros Mountains in the northeastern portion of the basin are highly structured and are the site of recent earthquake activity (Fig. 2). Prolific oil and gas seepages in this region of Iran and Iraq resulted in numerous oil discoveries (5). South and southwest into the Mesopotamian Valley, the sediments are characterized by much less deformation with only moderate seepage (16). The Arabian platform in the southwesternmost portion of the basin shows no recent earthquake activity, exhibits little recent structuring, and has little or no seepage (17). Ghawar, the world's largest oil field, is on the Arabian platform of the Persian Gulf basin. Correlation exists not between the size of commercial petroleum reserves and seepage activity but rather between the degree and timing of geologic structuring and seepage activity.

Other examples also confirm the correlation between seepage and structuring. Southern California and southern Alaska have high seepage, are highly structured, and have experienced considerable recent earthquake activity. By contrast, western Canada and the Sirte basin in Libya show little recent structuring or earthquake activity and have low present-day oil seepage.

Information on the types of structuring and the relative deformation of the marine areas is substantially more complete than information on seep frequencies or flow rates. As a result, the differences in structuring along continental margins in conjunction with the available data on seeps provide a more comprehensive basis for estimating the amount of petroleum seeping into the sea.





#### **Geologic Considerations**

Several geologic assumptions are required for estimating marine seepage:

1) More seeps exist in offshore basins than have been observed.

2) Factors that determine the total seepage in an area (number of seeps per unit area and the daily rate for each seep) are related to the structural style of the area and to the stage of basin evolution. On the basis of geologic concepts of basin evolution and geochemical knowledge on the origin, generation, migration, and alteration of oil, it is anticipated that seepage rates vary with time.

3) Within each structural style, seepage (both the number of seeps and, to a lesser extent, the average seepage rate) is primarily dependent on the area of rock and not on volume, provided that there is sufficient sediment volume and organic matter for the maturation and generation of petroleum. The area available for intersection with faults, fractures, and other potential migration pathways as well as for truncation and breaching of reservoirs is more important than the total sediment volume.

4) Most marine seeps are clustered along the continental margins in areas where a certain minimum thickness of sediments is exceeded. This assumption is based on the geochemical concept that a certain thickness of sediment is required before hydrocarbons can be generated from the source rocks.

5) Seepage rates have a log-normal distribution. There are many seeps with low flow rates but only a few with high individual rates; however, these provide much of the total seepage. The log-normal distribution of seepage rates is consistent with observations of field sizes, well-producing rates, basin hydrocarbon reserves, and the organic content of sediments, all of which are log-normally distributed.

We have used the geologic criteria listed in Table 1 in conjunction with geologic interpretations to classify the continental margins according to their potential for seepage. Maps of sediment thickness (18) were used to delimit areas of potential seepage; a minimum thickness of 3000 feet (which eliminates most of the world's deep ocean basin area) was used in this study. Figure 3 shows the classification of the continental margins and the area of each with at least 3000 feet of sediment thickness. However, oil is much more likely to generate and migrate

Table 2.	Sediment	thickness	and	maturation
factors f	or seepage	e-prone an	reas.	

Percentage of area > 20,000 feet thick	Percentage of area > 10,000 feet thick	Factor
> 60		1.0
50-59		0.9
4049	> 60	0.8
3039	50-59	0.7
20-29	40-49	0.6
10-19	30-39	0.5
5-9	20-29	0.4
1-4	10-19	0.3
	5-9	0.2
	0-4	0.1

and, hence, seep in areas where there are thicker sediments. For young sediments, the required thicknesses may be as great as 10,000 to 20,000 feet. Thus, all areas of potential seepage are not equivalent geochemically, even if they are of similar structural styles. Because of these variations, maturation and sediment thickness factors were determined and are listed in Table 2. The maturation factors were then applied to the various continental margin areas to determine the effective seepageprone area of each.

Offshore southern California meets the geologic criteria for high seepage potential. It is an area of high structural complexity dominated by strikeslip faulting and has experienced considerable earthquake activity and recent structural deformation. Estimates by different workers (10) for seepage in the nearly 1000-square-mile (2600square-kilometer) area from Point Conception to Point Fermin range from 100 to more than 900 barrels per day with some indication of seasonal variability. Although the estimated rate of 100 barrels per day for the entire 1000-square-mile area (19) may be conservative because other seeps, for example, eight to ten seeps in Santa Monica Bay, are estimated to flow at 10 barrels per day (9), the flow rate of 900 barrels per day for the Coal Oil Point seep alone (20) may not represent a sustained annual flow rate. However, evidence suggests that very high seepage flow rates might be

caused by a geologic "catastrophe" such as a major earthquake and might exist at least temporarily. In the calculations that follow, the lower rate of 100 barrels per day is used.

The stable, central portion of the western Canadian basin at the present time meets the geologic criteria for low seepage potential despite the presence of the Athabasca tar sands, which attest to the existence of substantially higher seepage rates in the past. The basin lacks significant recent strike-slip faulting or compression, is not highly structured, and has a low incidence of earthquake activity. The terrane and geology of this basin are well known, and it is unlikely that any large seeps exist which have not been found and reported. These observations (10) suggest that seepage here is approximately 0.1 barrel per day per 1000 square miles. Flow rates in areas of low oil seepage potential may even approach zero, as appears to be the case in the Sirte basin of Libya and the Permian basin of western Texas.

The classification of areas of moderate seep potential both onshore and offshore is based on the relative extent to which the various geologic conditions are met by comparison with the case for seep areas of high and low potential. Relative to areas of high seep potential, they exhibit lesser degrees of structural complexity and recent earthquake activity. However, areas of moderate seep potential possess the required geologic criteria for seepage to a greater degree than areas of low seep potential. For example, in the Persian Gulf, the Mesopotamian Valley with some reported seeps (and located between the high seep potential Zagros Mountains and the low seep potential Arabian shield) is interpreted as an area of moderate seep potential. Other onshore areas of moderate seep potential and with known seeps are the North Slope of Alaska and Magdalena Valley of Colombia. There are no reported measurements of seep flow rates from these areas, but it is assumed that the rates will fall between those of high and low seep potential localities.

Table 3. Mean seepage rates (in barrels per day per 1000 square miles).

Seepage	Type locality	Mean seepage rate		
potential of area	seepage rate	$\overline{\begin{array}{c} \text{Case I,} \\ P_{16} \end{array}}$	Case II, $P_{1.0}$	Case III, $P_{0.1}$
High	100	82	7.8	20
Moderate	3	2.45	0.048	0.010
Low	0.1	0.082	0.008	0.002



#### Calculations

To determine marine seepage, we used flow rates of 100 barrels per day per 1000 square miles for areas of high seepage, 3 barrels per day per 1000 square miles for areas of moderate seepage, and 0.1 barrel per day per 1000 square miles for areas of low seepage (1 barrel = 42 gallons or 160 liters). The high and low rates are taken from the southern California and western Canadian examples, respectively, and it is assumed that seepage in areas of moderate potential is the geometric mean of the high and low rates. For log-normal distributions, the geometric mean is the median; it is lower than the arithmetic mean.

Although the geologic conditions for "high," "moderate," and "low" localities match those for the "type localities," for example, southern California and western Canada, it is unknown whether the flow rates selected are typical of such areas. These rates are based on observations and will be in the statistical population of rates; they may fall anywhere within the distribution curve. However, since well-production rates and seepage rates are a function of many of the same parameterspermeability, pressure, drive mechanism, and API gravity (21)-this curve is assumed to be log-normal with a slope based on well-producing rates from major oil fields.

Total seepage estimates can be made on the assumption that the above rates fall at different points within the lognormal distribution. After the results were examined in the light of current geologic and geographic knowledge, it became apparent that, to obtain reasonable estimates of total seepage, the rates (in barrels per day per 1000 square miles) must fall in the lowprobability end of the distribution. Thus, three probability levels were considered— $P_{16}$ ,  $P_{1.0}$ , and  $P_{0.1}$ —for each of the three seepage areas. From the resulting curves, mean seepage rates for areas of high, moderate, and low seep potential were derived (Table 3).

For the total seepage calculations, the area in each of the "high," "moderate," and "low" potential localities was summed (Table 4) and then multiplied by the various statistically calculated mean flow rates (Table 3). The world total and regional breakdown (in  $10^6$  metric tons per year) for the Table 4. Seepage-prone areas of the world's oceans.

	Number of 1000-square-mile areas of		
Ocean	High potential seepage	Moderate potential seepage	Low potential seepage
Pacific	568	2715	1241
Atlantic	381	3030	3289
Indian	145	2318	880
Arctic		1648	718
Southern		142	134
Total	1094	9853	6262

Pacific, Atlantic, Indian, Arctic, and Southern oceans are summarized in Table 5.

#### Interpretation

Determination of annual marine seepage depends on how well the southern California and western Canada seepages represent the other 1000square-mile areas of similar geology in the world.

In case I in Table 5 we consider the three flow rates at the 16 percentile, which yield an estimated seepage of  $6 \times 10^6$  metric tons per year (113,000 barrels per day). This value appears to be near an upper limit on the basis of present knowledge. In this case it is required that there be 175 blocks of 1000 square miles each where the seepage is 100 barrels per day, the rate used for offshore southern California. There is a body of opinion (20) in support of the idea that seepage rates in southern California exceed 400 barrels per day and may approach 1000 barrels per day. If these higher rates for California are correct, then it is possible that either 175 undocumented 1000-square-mile areas with seepage rates of 100 barrels per day or fewer areas with higher rates may exist.

Case II places the type locality flow rates at the 1.0 percentile and yields an annual worldwide marine seepage of  $0.6 \times 10^6$  metric tons per year (11,300 barrels per day). The 1.0 percentile means that in 99 out of 100 areas of high, moderate, and low potential seepage the flow rates will be less than 100, 3, and 0.1 barrels per day per 1000 square miles, respectively. In this case the mean flow rates for high, moderate, and low seepage areas are approximately 8, 0.05, and 0.008 barrels per day per 1000 square miles, respectively (Table 3, case II). For example, this estimate requires that there be 11 1000-square-mile offshore areas in the world with flow rates of 100 barrels per day. Observations suggest that flow rates of 100 barrels per day per 1000 square miles may occur in offshore portions of Trinidad, eastern Venezuela, and Ecuador-Peru (22). If the seepage rate for southern California is in fact in the range of 400 barrels per day, then even fewer high seep areas would be required to meet the conditions of this case. On the basis of the various geologic and geochemical considerations outlined as well as the limited seep data available, the estimate of  $0.6 \times 10^6$  metric tons per year appears highly reasonable. This estimate recognizes that offshore California and western Canada are geologically representative of high and low potential seep areas, respectively. However, it indicates that their seepage rates are not typical but have a probability of only 1 in 100 of occurring elsewhere in the world. In this regard, this estimate, although considered most reasonable, may be somewhat conservative (23).

Case III, with flow rates at the 0.1 percentile, yields a minimum estimate. This case places the rate of 100 barrels per day per 1000 square miles as the highest seepage rate worldwide. Since actual seepages in the southern California area may be higher than the assumed value, and at least a few other areas equivalent to southern California apparently exist, the calculated estimate of  $0.2 \times 10^6$  metric tons per year (3800 barrels per day) represents a minimum figure.

Any seepage estimate must be ex-

Table 5. Summary of worldwide seepage rates: regional breakdown by oceans (in 10<sup>6</sup> metric tons per year).

Ocean	Case I, $P_{16}$	Case II, $P_{1,0}$	Case III, $P_{0,1}$
Pacific	$2.83 \times 10^{6}$	$2.69 \times 10^{5}$	$0.689 \times 10^{5}$
Atlantic	$2.06 \times 10^{6}$	$1.96 \times 10^{5}$	$5.04 \times 10^{4}$
Indian	$9.30 \times 10^{5}$	$8.85 \times 10^{4}$	$2.28 \times 10^{4}$
Arctic	$2.14 \times 10^{5}$	$2.30 \times 10^{3}$	$5.20 \times 10^3$
Southern	$1.88 \times 10^4$	$1.74 \times 10^{3}$	$4.51 \times 10^{2}$
Total	$6.05 imes10^{6}$	$0.558  imes 10^5$	$0.148 \times 10^{\circ}$

amined to determine if annual seepage rates are realistic in terms of the volumes of hydrocarbons available for seepage and the rates at which hydrocarbons are being generated in the source rocks. It is generally accepted that petroleum is formed from organic matter contained in fine-grained source rocks and then is mobilized and expelled from these rocks. Calculations based on the work of Hodgson et al. (24) indicate that only 1 percent of the mobilized hydrocarbons may have been trapped in oil reservoirs. Oil mobilized from source beds and not trapped will eventually be lost through seepage. Therefore, a much larger amount of petroleum will be lost to seepage than will ever be trapped in reservoirs.

Weeks (25) has estimated the world's potential offshore reserves occurring in water depths of 1000 feet or less to be  $630 \times 10^9$  barrels of oil recoverable by primary production methods. Recent work by Albers et al. (26) indicates a minimum of over  $800 \times 10^9$ barrels recoverable out to water depths of about 600 feet. Weeks has noted that 80 to 90 percent of the presently discovered oil is found in Mesozoic and Tertiary rocks and that a similar percentage can be anticipated in rocks of the same age in the off-shore areas.

Recoverable reserves constitute only a portion of the oil in place in the reservoir. If one-third of the oil in place is recoverable, the estimates of Albers and Weeks represent approximately  $2 \times 10^{12}$  barrels of oil in place in the reservoir. Since this volume may represent only 1 percent of the oil mobilized from the source bed, the amount of oil available for seepage reflected by these reserve estimates is about  $2 \times 10^{14}$  barrels or nearly  $3 \times$ 1013 metric tons. This volume of oil alone could have sustained a seepage rate of  $0.6 \times 10^6$  metric tons per year (case II) for  $50 \times 10^6$  years or for a time span equivalent to most of the Tertiary. However, the total oil available for seepage and the time span would be substantially greater since the reserve estimates of Albers and Weeks are limited to water depths up to 600 and 1000 feet, respectively. These water depths include less than half of the offshore area that is considered to be seepage-prone. Moreover, the above reserve figures do not include oil from tar sands and oil shales, which are also potential seepage sources. The addition of available oil from the greater water depths and the inclusion of all potential seepage sources would sustain the seepage rate of  $0.6 \times 10^6$  metric tons per year for a period of time equivalent to the Tertiary and much of the Mesozoic.

Obviously such a calculation as the above does not necessarily confirm either the estimated annual marine seepage rate of  $0.6 \times 10^6$  metric tons per year or the probable range of seepage volumes. The generation, migration, entrapment, and seepage of oil is a dynamic process that is currently under way and has been continuing throughout much of geologic time. There is no evidence to suggest that past marine seepage rates are the same as at present. It seems likely that, as a result of changing conditions through geologic time, marine seepage rates may have had considerable variation. Whether present geologic conditions are indicative of average or extreme rates, either high or low, is unknown. However, this calculation does support the reasonableness of the estimate in that it suggests that the natural system could accommodate the present marine seepage of  $0.6 \times 10^6$  metric tons per year over a period of geologic time comparable to that of the Tertiary and much of the Mesozoic when a large percentage of the offshore oil was being generated.

#### Conclusions

The probable range of seepage into the marine environment is  $0.2 \times 10^6$  to  $6.0 \times 10^6$  metric tons per year. Within this range the best estimate for the present marine seepage worldwide is on the order of  $0.6 \times 10^6$  metric tons per year. This estimate is based on the presumption that only a few other areas around the world are as seepage-prone as southern California. Measurements of seeps and seepage rates are too few to allow an accurate estimation by observation and measurement techniques alone. Seepage potential can, however, be related to geologic criteria, and these provide sound bases for marine seepage assessment.

On the basis of this estimate, areas of high seepage potential contribute about 45 percent of the worldwide seepage, areas of moderate seepage about 55 percent, and areas of low seepage less than 1 percent. The situation varies somewhat from ocean to ocean. In the Pacific Ocean, areas of high seep potential are by far the major contributors. In the Atlantic, Indian, Arctic, and Southern oceans, areas of moderate seep potential are most significant because areas of high seep potential are relatively rare in these realms. The circum-Pacific area is the area of greatest seepage; it contributes about 40 percent of the world's total.

#### **References and Notes**

- 1. Seeps can be either "visible" or "nonvisible." The escape of petroleum or petroleum hydro-carbons through microseeps associated with faults or fractures and by diffusion from compacting sediments represents an important source of hydrocarbons in seawater. It leads to hydrocarbon anomalies which are detectable only in the composition of marine bot-tom waters or sediments. These "nonvisible" sources are also included in our estimates, although the text descriptions are necessarily confirmed to "visible" seeps.
- confirmed to "visible" seeps. 2. This estimate does not include "detrital oil" derived from land sources such as onshore breached petroleum reservoirs or from the subaerial erosion of tar sands, asphalts, and source rocks containing minutely disseminated liquid petroleum. Although all of these are potential natural sources of hydrocarbon inputs into the oceans, they are not inputs directly from marine seepage but are contributed indirectly by erosion and river runoff.
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SCIENCE, VOL. 184

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## **Chromatin Structure: Oligomers of the Histones**

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The histones comprise an  $(F2A1)_2(F3)_2$  tetramer, a different oligomer of F2A2 and F2B, and monomer of F1.

Roger D. Kornberg and Jean O. Thomas

Biochemical and x-ray diffraction results concerning the oligomeric structure of the histones are presented. The results show pairwise associations in solution, two types of histone forming a tetramer and two other types of histone forming a different oligomer. The same pairwise associations appear to occur in chromatin.

#### **Introduction to the Histones**

There are five main types of histone in the chromatin of eukaryotes, known as F1 (or I) with a mass of 21,000 daltons; F2A1 (or IV), of 11,300 daltons; F2A2 (or IIb1), of 14,500 daltons; F2B (or IIb2), of 13,700 daltons; and F3 (or III), of 15,300 daltons. There are usually nearly equimolar amounts of all the histones except for 24 MAY 1974

F1, of which there is about half as much (1).

The arrangement of histones and DNA in chromatin has been studied by x-ray diffraction (2, 3), leading to the proposal (4) of a "super-coil" model. The x-ray data have not been sufficient, however, to prove the validity of the model. Various studies have been undertaken to supplement the x-ray data, such as studies of the association behavior of the histones (5-7) and studies of complexes of one or another type of histone with DNA (6, 8). In most cases, histones purified to homogeneity from calf thymus were used. Four of the histones, F2A1, F2A2, F2B, and F3, were observed to form large self-aggregates. For example, F2A1 and F3, at pH 7 and ionic strength 0.1, form self-aggregates of sedimentation coefficient 19S and molecular weight about 106. Such aggregates may be the cause of anomalous stoichiometries in complexes of the histones with DNA. For example, five to ten times as much F2A1 will bind to a given weight of DNA as is bound to the same weight of DNA in chromatin.

#### **Oligomers of the Histones in Solution**

The tendency of histones to form large aggregates may be a consequence of the denaturing conditions under which they are prepared. The histones are usually extracted from chromatin in acid and fractionated by ethanol and acetone precipitation, followed by gel filtration in acid or by ion-exchange chromatography in guanidine hydrochloride. We decided to try milder methods and, in particular, the procedure of van der Westhuyzen and von Holt (9), which involves extracting the histones from chromatin in 2M sodium chloride-50 mM sodium acetate (pH 5) and fractionating the extract by Sephadex G-100 gel filtration in 50 mM sodium acetate at pH 5. The Sephadex G-100 elution profile consists of two peaks, both coming after the excluded volume and thus of molecular weight less than about 105. The first (higher molecular weight) peak contains F1, F2A1, and F3; and the second (lower molecular weight) peak contains F2A2

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