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Pattern of first and last appearance in diatoms: Oceanic circulation and the position of polar fronts during the Cenozoic

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Pattern of first and last appearance in diatoms: Oceanic circulation and the position of polar fronts during the Cenozoic

Abstract
First and last occurrences of 389 diatom species from the first global Cenozoic record are used to reconstruct the position of major oceanographic boundaries. First appearances and extinctions group in three latitudinal bands: middle to high northern latitudes, equatorial region, and high southern latitudes. Sparse Paleogene occurrences were limited to southern high latitudes along the equivalent of the modern Antarctic polar front. Its late middle Eocene to middle Miocene position varied within 10°, and within a 20° band from middle Miocene to present, suggesting an association with global cooling. First and last occurrence events appear in the two remaining latitudinal regions during the Eocene and increase in a stepwise fashion, mimicking significant cooling events. At about 16 Ma, first and last appearances shift from the North Atlantic to the North Pacific. Low-latitude data suggest low surface water productivity prior to 40 Ma, while increased abundance from the middle Miocene correlates with expansion of the east Antarctic Ice Sheet.

Keywords
diatoms, evolution, paleoceanography, oceanographic boundaries, Antarctic polar front, Cenozoic

Disciplines
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Pattern of first and last appearance in diatoms: Oceanic circulation and the position of polar fronts during the Cenozoic

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[1] First and last occurrences of 389 diatom species from the first global Cenozoic record are used to reconstruct the position of major oceanographic boundaries. First appearances and extinctions group in three latitudinal bands: middle to high northern latitudes, equatorial region, and high southern latitudes. Sparse Paleogene occurrences were limited to southern high latitudes along the equivalent of the modern Antarctic polar front. Its late middle Eocene to middle Miocene position varied within 10°, and within a 20° band from middle Miocene to present, suggesting an association with global cooling. First and last occurrence events appear in the two remaining latitudinal regions during the Eocene and increase in a stepwise fashion, mimicking significant cooling events. At about 16 Ma, first and last appearances shift from the North Atlantic to the North Pacific. Low-latitude data suggest low surface water productivity prior to 40 Ma, while increased abundance from the middle Miocene correlates with expansion of the east Antarctic Ice Sheet.

INDEX TERMS: 3030 Marine Geology and Geophysics: Micropaleontology; 4267 Oceanography: General: Paleocenography; 4855 Oceanography: Biological and Chemical: Plankton; 9604 Information Related to Geologic Time: Cenozoic; KEYWORDS: diatoms, evolution, paleoceanography, oceanographic boundaries, Antarctic polar front, Cenozoic


1. Introduction

[2] A question raised by paleoceanographers is when, and under what conditions, did present-day oceanographic fronts develop? Obviously, some are dictated as a consequence of Earth’s rotation. However, in higher latitudes oceanographic fronts have a different history and their location appears to be dictated by climate, submarine topography, the changing positions of continents, the coupling and decoupling of global ocean segments and the flux of fresh water into the ocean via icebergs and melting sea ice. Here we relate the geologic history of the first and last appearance of planktonic diatoms to oceanic circulation changes and the development of fronts during the Cenozoic. Much of our focus is on high latitudes but we also include reference to lower latitudes where it can provide a clue to higher latitude paleoceanography. Similarly, we point out where plate motion may have played a role in obscuring or blurring the record of diatom occurrence. Our study is based on a compilation of Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) diatom data up to Leg 135 (1968–1994) [Spencer-Cervato, 1999].

[3] As the oxygen isotope record for the latest Cretaceous and Cenozoic indicates [Miller et al., 1987; Zachos et al., 2002], global ice volume increased in a series of punctuated steps. Further, field evidence has shown that, save for the past 3 to 4 million years, most of this increase occurred on Antarctica. Although some argue for the existence of a continuous ice cap on Antarctica since the beginning of the middle Eocene [Prentice and Matthews, 1988], the oldest generally accepted evidence for glaciation places it in the Oligocene. A few studies, however, extend ice sheets back to the late middle Eocene [Barron et al., 1991]. Isotopic and sequence records indicate that ice volume changes in Antarctica affected global sea level by at least 43–42 Ma [Browning et al., 1996]. Since at least ~36 Ma, the Southern Ocean has acted as a major sink for biogenic opal, reflecting increased surface water productivity resulting from cooling and upwelling in the circum-Antarctic [Brewster, 1980; Baldauf et al., 1992; Lazarus and Caulet, 1993; Salamy and Zachos, 1999].

2. Methods of Study

[4] Micropaleontological data from 165 Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) sites were included in the Neptune relational database [Lazarus et al., 1995; Spencer-Cervato, 1999]. The chronologies of these sites are based on biostratigraphy and magnetostratigraphy [Lazarus et al., 1995; Spencer-Cervato, 1999] and are calibrated to the Berggren et al. [1995] timescale. Range
chart data, species’ presence/absence in analyzed samples, and abundance (if available) published in the Initial Reports of the DSDP and ODP and the Scientific Reports of the ODP constitute the micropaleontological information in \textit{Neptune}. Taxonomic revision of all species’ names included in all published DSDP range charts (some 8000 marine plankton species names) and the selected subset of ODP range charts (some 4000 additional names) was done according to the most recent and widely accepted taxonomy published in the literature for the \textit{Neptune} database. Valid species names were identified and their synonyms linked to them. Searches were done for occurrences of valid species names (with linked synonyms) in the 165 sites with chronological control. The age and location (DSDP/ODP holes) of the oldest (first appearance datum (FAD)) and youngest (last appearance datum (LAD)) occurrences were extracted. Unless otherwise documented, species that occurred in recent samples (<0.5 Ma) were considered extant.

Species occurring in at least two holes were included in the final compilation on which this study is based. This selection was necessary to minimize the potential bias given by species recorded in only one hole, and, as such, often taxonomically not well defined. The geographic position of the site at which the FAD or LAD event was recorded was backtracked using a PC-based program kindly provided by Alan Smith (Cambridge University) which uses finite rotations. The program is based on published reconstruction data (Euler rotations and their ages) used to move a given site relative to Africa and then reposition that site in paleomagnetic coordinates (A. Smith, personal communication, 1997). Paleopositions were estimated at 5 million year (myr) intervals, backtracking them from their present position (age 0). The paleogeographic positions of the FADs and LADs are therefore approximated to the nearest 5 myr interval. This approximation does not significantly affect the data, as the rate of movement of tectonic plates within 5 myr is usually comparatively low.

A total of 389 diatom species are included in this study. Their temporal range (longevity) was determined by subtracting the LAD age from the FAD age and is expressed in millions of years (myr). The range of the 103 extant species in this compilation represents a minimum estimate. Since this is a compilation of results of many diatom workers, the reader should be aware that no standard diatom preparation process was used. However, we assume that each worker prepared samples in such a way as to recover a significant portion of the flora. Further, we emphasize that our results represent a compilation of DSDP/ODP diatom data up to Leg 135 [Hawkins et al., 1994] and does not include Mesozoic diatom occurrences which are spotty and not well represented. We recognize that data recovered from later ODP legs may modify our conclusions. However, we also recognize that there should be a cutoff point, at which one must stop and publish one’s findings. The \textit{Neptune} database is currently being upgraded to include post-Leg 135 and Mesozoic data but we do not expect that this will be accomplished before the end of 2004. We also point out that prior to DSDP Leg 16 [Bukry and Foster, 1973], diatoms were not included in the initial reports although others have since written about some of these earlier cruises [e.g., Barron, 1985]. The raw data used for this study are available at the World Data Center-Paleoclimate data repository (http://www.ngdc.noaa.gov/paleo/paleo.html).

3. Temporal and Spatial Distribution of Diatoms

Molecular biological evidence suggests that diatoms, or the clade that led to them, appear to have first evolved in the early Mesozoic [Medlin et al., 1997]. Although diatoms are reported in sediments as old as the pre-Cambrian [Witkowski and Sieminska, 2000], the oldest agreed upon marine diatom assemblages are found in sediments of Cretaceous age. Late Cretaceous marine diatoms have been found in California [Hanna, 1927; Long et al., 1946], northern Urals [Jousé, 1951], Kunashir Island in the Kuriles [Jousé, 1963; Strelnikova, 1974], the Koryak Upland in the Russian Far east [Strelnikova, 1974], the eastern United States [Abbot, 1978], the southwest Pacific [Hajos and Stradner, 1975], while early Cretaceous marine diatoms have been recovered from the south Atlantic [Harwood and Gersonde, 1990; Gersonde and Harwood, 1990], and in the eastern equatorial Indian Ocean. Strelnikova [1974] reported Cretaceous diatoms from various locales in the former USSR and Hajos and Stradner [1975] reported on a very diverse and well preserved flora from the south Pacific, as did Harwood [1988] from Seymour Island off the Antarctic Peninsula. Diatoms have also been reported in Cretaceous sediments from such diverse locales as the midcontinent of the United States, British Columbia (Canada), Queensland (Australia), and the Arctic Ocean. Despite the controversy on time of first appearance of marine diatoms, it seems apparent that the first appearance of assemblages occurred during the Cretaceous and very likely during the early to middle Cretaceous. We note that, based upon published literature to date, higher latitude Cretaceous assemblages had the highest diversity whereas lower diversity assemblages occur in low to mid latitudes. This might suggest that diatoms first appeared in high latitudes. Further, their absence from known Jurassic deep-water facies that we have examined may suggest that they emerged in shallow marine waters during the Jurassic and subsequently spread into open ocean (planktonic) environments.

4. Diatoms and Fronts

The distribution and abundance of diatoms as well as the enumeration and statistical treatment of species have been used for paleoceanographic reconstructions [Armand, 1997, 2000; Burckle, 1984; Crosta et al., 1998]. At the most basic level, high diatom abundance or even diatom occurrence in surface sediments can be correlated with overlying regions of high surface water productivity (Figure 1). Diatoms in sediments occur, for example, on the highly productive eastern side of the equatorial regions and are usually absent or in low abundance on the less productive western side. Further, they are largely absent from sediments beneath central water masses where surface water productivity is low. Figure 1 shows major diatom-occurrence zones in surface sediment: a southern belt between 45° and 65°S, a northern high-latitude belt, and an equatorial belt. Diatoms
Figure 1. Diatom presence/absence in surface sediments of the world’s ocean. Data are based upon smear slide analysis of cores curated at the Lamont-Doherty Earth Observatory and the Antarctic Facility at Florida State University.
also occur in sediments beneath the eastern and western boundary currents in the Pacific and Atlantic Oceans. A similar pattern exists for the first (FAD) and last (LAD) appearance data collected for this study (Figure 2) suggesting that the spatial distribution of FADs and LADs of planktonic diatoms reflect high surface water productivity zones. Such data further suggest that the location of planktonic diatoms’ FADs and LADs may be used to track, over the long term, oceanographic frontal history. Species can tolerate a certain range of environmental conditions, in part by the development of different phenotypes in response to different local conditions, in part by differently adapted genotypes within the overall population (D. B. Lazarus, manuscript in preparation, 2002). However, when the limits of a species’ adaptation are reached, the species becomes extinct. It is therefore to be expected that the extinction and appearance of diatom species will mark the geographic boundary that represents the environmental limits of tolerance, such as an oceanographic front and boundaries of high surface water productivity.

5. Results and Discussion

The FAD and LAD of diatom species are presented in separate graphs. However, the results do not show a substantial difference in temporal or spatial distribution and the FADs and LADs are therefore discussed together. Their distribution by latitude is shown in Figure 2. The data show three discrete clusters; one in middle to high northern latitudes (20° to 65°N), one in low latitudes (between 10°N and 15°S) and a third in high southern latitudes (45° to 75°S). Within this latter cluster, over 90 FADs and 68 LADs occur between 55° and 60°S. The distribution of these events versus age during the Cenozoic is shown in Figure 3.

Paleocene FAD and LAD events are restricted to a narrow latitudinal band in high southern latitudes. Among these 37 species, some were short-lived and presumably endemic to high southern latitudes (e.g., *Grunowiella gemmata*, *Grunowiella palaeocaenica*, *Hemiaulus peripterus*, *H. rossicus*), whereas others were extremely long-lived and had a much broader geographic distribution (e.g., extant species *Paralia sulcata* and *Stephanopyxis turris*; Figure 4). No FADs or LADs were recorded between approximately 55 and 46 Ma. At 46 Ma, diatoms appear at mid to high northern latitudes and the number of FADs increases. Shortly after, FADs and LADs are also recorded at low latitudes. After about 32 myr, extinctions are spread more or less evenly throughout the three geographic clusters.

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**Figure 2.** Histogram of the distribution of diatom (a) FADs and (b) LADs by latitude. Southern latitudes are expressed as negative values. Paleolatitude positions were obtained through backtracking as described in the text.

**Figure 3.** Graph showing the age of diatom (a) FADs and (b) LADs in million years versus the latitude at which they were found. Paleolatitude positions were obtained through backtracking as described in the text.
The concentration of diatom FADs and LADs in the Southern Ocean during this time is consistent with these results. Beginning in the latest early Eocene, the thermocline weakened in tandem with a global cooling trend. This may have been accompanied by a lowering in surface water productivity consistent with the absence of diatom speciation between 55 and 40 Ma.

[12] Browning et al. [1996] inferred the earliest occurrence of Antarctic glaciation at 42 Ma from North Atlantic sea-level data. Long-term and punctuated cooling associated with increased ice buildup in Antarctica continued through the Oligocene and early Miocene. The early middle Miocene (16–15 Ma) is characterized by cooling of bottom waters [Miller et al., 1987], increased ocean vertical temperature gradients, and major expansion of the east Antarctic Ice Sheet [Kennett, 1985]. We interpret the increase in FAD and LAD abundance around 42 Ma in the Southern Ocean as an indication that the polar front zone became well established at that time and influenced surface water productivity. If we infer that the southernmost region at which most planktonic diatoms speciated or became extinct is in the vicinity of the APF, its position has varied within a 10° band from the late middle Eocene to the middle Miocene and within a 20° band from middle Miocene to present. This suggests that broader fluctuations in the position of the polar front high productivity region are associated with global cooling events.

[13] Recall that oxygen isotope data for the Cenozoic strongly suggest that there was a major enlargement of the east Antarctic Ice Sheet (EAIS) at around the early/middle Miocene boundary [Miller et al., 1987]. Recall also that the west Antarctic Ice Sheet (WAIS) developed during the late Miocene/early Pliocene [Shackleton and Kennett, 1975] although it may have made episodic appearances before then. The Last Glacial Maximum (LGM)/Holocene difference in the location of the polar front is greatest in the Atlantic sector. We suggest that linking the Antarctic Peninsula to the EAIS by building the WAIS provided the means for the northward expansion of the polar front as well as the northward expansion of sea ice and iceberg tracks (and low-salinity tongues). The Southern Ocean must have been different without the WAIS, particularly in the Atlantic sector. In the Pacific sector, on the other hand, there is not a great difference in the location of the APF between the LGM and the Holocene. In the Indian Ocean, the LGM/Holocene difference is somewhat intermediate between the Atlantic and Pacific Oceans.

[14] In high northern latitudes, the pattern of diatom FADs and LADs is less distinct than in the Southern Hemisphere probably owing to the concentration of continental masses, causing the development of a more complex pattern of net local upwelling, which has a greater influence on the position of the Arctic polar front as reflected by the present conditions (Figure 1). The boundary of diatom speciation peaks at mid latitudes between 35°N and 45°N, but the data are spread between 20°N and 65°N and fit in two clusters separated at around 30–35°N (Figures 3 and 4). With few exceptions, no FADs and LADs are recorded in this region prior to 35 Ma. Sporadic Oligocene to early Miocene events are

Figure 4. Longevity in million years of diatom (a) FADs and (b) LADs versus their latitudinal position. Paleolatitude positions were obtained through backtracking as described in the text.

further increase in FAD and LAD occurrences is recorded from the middle Miocene at about 14 myr. Two thirds of the extant diatom species in this study had their FAD within the past 15 Ma. The remaining one third appeared between the early Paleocene and middle Miocene.

5.1. High and Midlatitudes

[11] First and Last Appearance Datum levels during the Paleocene are found only in high southern latitudes. Their latitudinal distribution (Figures 3 and 4) suggests that, since at least the early Cenozoic, an oceanographic front, most likely the equivalent of the modern-day Antarctic polar front (APF) at least in its surface expression, was present between about 50°S and 65°S. This finds support in the study of Stott et al. [1990] who used planktonic foraminiferal stable isotope values to reconstruct Southern Ocean surface water structure during the Paleogene. Stott et al. [1990] inferred that a seasonal thermocline was well developed in the Southern Ocean during the late Paleocene and early Eocene, resulting in high spring/summer surface water productivity.

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recorded exclusively in the north Atlantic (Figures 5 and 6). After 16 Ma, speciation and extinction events shifted to the north Pacific. In the modern ocean, diatoms are particularly abundant in the nutrient-rich north Pacific Ocean. Our data indicate that this situation has been quite stable and active since the middle Miocene, while prior to that time, surface waters were more productive in the north Atlantic.

We also point out that some of the FADs in the North Pacific are more likely due to plate motion rather than evolutionary events. This is true of the middle to high-latitude North Pacific where diatom FADs occur at about 14 Ma. The reason for this is that the plate upon which the sites were located transited from beneath the less productive central water mass to beneath the more productive Kuroshio Current. Most of the DSDP sites crossed this boundary at about the middle Miocene. Time slice maps of diatom occurrence during the Neogene of the North Pacific (L. Burckle, unpublished data, 2002) show that present-day circulation became established at around the early/middle Miocene boundary (i.e., the time of build up of the east Antarctic Ice Sheet). During the early Miocene, the central water mass was much expanded and diatoms only occurred around the periphery of the North Pacific. Diatoms are

Figure 5. Diatom FAD data versus latitude shown in Figure 4 subdivided into ocean basins: (a) Atlantic Ocean, (b) Indian Ocean, and (c) Pacific Ocean. LAD/FAD age versus LAD/FAD latitude in Atlantic, Indian, and Pacific Oceans.

Figure 6. Diatom LAD data versus latitude shown in Figure 4 subdivided into ocean basins: (a) Atlantic Ocean, (b) Indian Ocean, and (c) Pacific Ocean. LAD/FAD age versus LAD/FAD latitude in Atlantic, Indian, and Pacific Oceans.
present on land sections adjacent to the North Pacific but are pyritized and difficult to identify to the species or even generic level.

5.2. Low Latitudes

[16] No diatom speciation or extinction is recorded in low latitudes prior to 40 Ma (Figures 3 and 4). This is interpreted as due to extensive dissolution prior to this time. However, diatom dissolution beneath what are presently considered to be productive areas also implies past low surface water productivity. This is consistent with Pearson et al. [2001] who argue that oxygen isotope evidence in support of colder than present equatorial waters during the Cretaceous and early Cenozoic is flawed. Such an interpretation of the data was at odds with modeling data, which called for warm tropical oceans during this time. Pearson et al. [2001] cite new isotopic evidence favoring a warmer (than present) tropics during this time interval. Such a warmer than present equatorial scenario implies that there was reduced upwelling of deep water during the Cretaceous and early Cenozoic in the equatorial regions (in contrast to the present). Therefore one would expect little or no diatom accumulation on the seafloor during this time, at least in low latitudes. Our data show that diatom FADs and LADs are absent from tropical latitudes during the Cretaceous and early Cenozoic and we attribute this to reduced equatorial upwelling and low productivity (note, however, the recent exchange between Zachos et al. [2002] and Pearson et al. [2002]).

[17] Between 40 and 30 Ma, a few diatom species originated in the equatorial and northern tropical Atlantic Ocean within two narrow latitudinal belts. Several species originated or became extinct during this time in the tropical Indian Ocean. Between 30 and 20 Ma, first appearances and extinctions are rare and confined to the tropical north Atlantic. The next increase in diatom speciation and extinction occurs around 15 Ma with most FADs and LADs limited to the Indian and Pacific Ocean. We interpret this as due to the mid-Miocene cooling contemporary with the expansion of the east Antarctic Ice Sheet. Oceanic circulation became more active at this time and more vigorous boundary currents caused the shrinking of midlatitudinal water masses in the Pacific.

[18] Indian Ocean circulation is somewhat different from the Atlantic and the Pacific leading to differences in diatom occurrence on the seafloor [Burckle, 1989]. This is due to surface circulation and to the presence of the hydrochemical boundary at about 10° south [Wyrski, 1973, Figures 3a–3d]. Burckle [1989] found that diatoms were present in surface sediments north of the hydrochemical boundary but not to the south of it. This is because the hydrochemical boundary is also a nutrient front. Nutrients are in low concentrations south of the front (hence few diatoms in bottom sediments) whereas they are in higher concentration north of the front (hence diatoms in bottom sediments). As in the North Pacific, the FAD of diatoms in the tropical Indian Ocean may be due to the fact that the plate upon which the DSDP/ODP site was located passed beneath the hydrochemical boundary. Hence an apparent first occurrence would be dictated by plate motion and not by an evolutionary or paleoceanographic event.

6. Conclusions

[19] We suggest that both dispersal from speciation centers and vicariance (i.e., subdivision of widespread ancestral species by the appearance of natural barriers) played roles in the evolution of diatoms. This is indicated by increases of both diatom speciation and extinction events in restricted geographic areas and at times when oceanographic barriers were created by development, expansion or shrinkage of water masses. We call on a number of factors to account for diatom distribution and evolution. For one, the global cooling that has taken place in punctuated steps during the Cenozoic. Similarly, the coupling of various remnants of Southern Hemisphere oceans to become the Southern Ocean, which thermally isolated high southern latitudes from lower latitudes resulting in the formation of a larger east Antarctic Ice Sheet [Shackleton and Kennett, 1975]. Further, the decoupling of the low-latitude ocean at the Panama Isthmus during the Pleistocene and the severing of the Tethys connection between the midlatitude Atlantic and the Indian oceans during the Miocene may have played a role.

[20] In addition to the joining of water masses, paleoclimatic and paleoceanographic events around Antarctica may have played a role in diatom evolution and extinction. Consider the history of the Southern Ocean. During the late Cretaceous and Cenozoic, it evolved from disconnected bodies of water to a single body that is physically heterogeneous. Later in its history it developed partial seasonal ice cover that influenced air-sea interactions and modified the temporal impacts and nature of vertical mixing processes. Further, it exhibits a vast range of seasonally varying physical properties (e.g., surface temperature, solar irradiance, wind stress), and hence became highly dynamic. Because the lowering sea surface temperature limits the absolute rates of biological reactions, biological processes in polar regions are more strongly impacted by physical processes than temperate or tropical waters. As a result of plate motion, the Cenozoic witnessed the formation of water mass boundaries (polar front, Subantarctic front, Antarctic divergence) as well as nutrient boundaries and the appearance of ice sheets, sea ice and icebergs. These latter two must have played a role in the freshwater/saltwater budget (thermohaline circulation, air/water interchange) as well as providing platforms for more species habitats and more FADs.

[21] Although we are less certain about the causes of extinctions, it is worth making a few points. Increased competition for nutrients and raw materials needed to build a shell may have played a role in diatom extinction. The ocean mass probably always been undersaturated with respect to silica. However, changes in climate, oceanography and the distribution of continents will frequently result in changes in the way that silica is parcelled out at different times in different oceans. This may have happened during the coupling of the Southern Ocean and the decoupling of the low-latitude oceans. It must have been particularly true...
for the higher latitude Southern Ocean because the oceanography was being put into place within the framework of the buildup of the EAS and eventually the WAIS. Consider also the fact that sea ice was forming and expanding during this time and intermediate and bottom water masses were developing.

One thing that may drive diatom evolution and diversity is the increase in the number of ecologic niches during the Cenozoic. The early Cenozoic is characterized by a large number of cosmopolitan species. This cosmopolitanism broke down as the Earth became cooler through the Cenozoic. There is no clear tie with paleoclimatic events but it seems reasonable to point out that as the Earth cooled off and more climatic zones and water masses developed, there would be more ecological niches developed. Some examples would be the similarity between the high and low latitudes during the early Cenozoic. By late Cenozoic times, the assemblages were largely dissimilar. More populations, more distinct gene pools to spur evolution. An interesting question for future studies may be why did some species hang on and maintain their bipolar life style?

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