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Earth and Planetary Science Letters 246 (2006) 367 – 380
EPSL
www.elsevier.com/locate/epsl

Simulating the impact of the Panamanian seaway closure on ocean circulation, marine productivity and nutrient cycling

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Received 13 October 2005; received in revised form 13 April 2006; accepted 15 April 2006
Available online 22 May 2006
Editor: M.L. Delaney

Abstract

The closure of the Panama Isthmus, ~14–3 Ma, caused large reorganizations of ocean circulation. Here we use a global climate–ocean ecosystem model to investigate the effects of the closing gateway on ocean circulation, marine productivity and nutrient distributions. Several sensitivity experiments with different sill depths and vertical diffusivities are performed. Consistent with previous model studies, we find constricted throughflow due to shallowing of the sill leads to intensification of the North Atlantic thermohaline overturning. We demonstrate a strong coupling between the flows through the tropical gateways of Panama and Indonesia in a way that reduced outflow of upper ocean Pacific waters via the Panama gateway into the Atlantic is compensated by increased flow through the Indonesian Archipelago. The simulated rates of North Atlantic Deep Water formation strongly depend on the vertical diffusion in the model, particularly for a deep sill. For the first time, we document by model results shifts in nutrient distributions associated with reorganizations of ocean circulation with repercussions on marine productivity patterns. Reduced flow of nutrient-rich sub-surface waters from the Pacific into the Atlantic reduces biological productivity in the North Atlantic. In the eastern tropical Pacific restriction of the nutrient-rich outflow leads to nutrient accumulation which in turn maintains a strong increase in productivity. These results seem to be largely consistent with the paleoproductivity proxy record. A massive drop of opal accumulation rates, however, as found in North Pacific sediments for the time of the final closure (~2.75 Ma) cannot be simulated. Generally, global marine net primary productivity (NPP) is found to increase with proceeding gateway closure.

Keywords: paleoceanography; ocean gateways; modelling

1. Introduction

The closure of the Panama Isthmus during the late Neogene, from about 14 until 2.75 Ma ago [1], caused large reorganizations of ocean circulation [2,3] with strong climatic impact. While the climate of the early to mid-Pliocene was characterized by higher temperatures than present and probably a stronger thermohaline circulation (THC) [4,5], a gradual cooling persisted during the late Pliocene [6], the reasons of which are still unknown. Striking is the temporal accordance of the final closure of the Panama gateway around 2.75 Ma with the intensification of the Northern Hemisphere glaciation (NHG). However, it is not clear whether the gateway configuration caused the onset of NHG [7], delayed [8] or preconditioned it [9,10].

Paleorecords from the Aratro Basin (NW South America) show the earliest strong indications for a restriction

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doi:10.1016/j.epsl.2006.04.028

of the deep Panama throughflow for the time period around 12 Ma ago [11] and a further shoaling of the seaway appeared around 8–6 Ma, when Atlantic and Pacific $\delta^{13}C$ records from benthic foraminifera began to diverge [2,12]. The first evidence for the restriction of surface water exchange between the Eastern Equatorial Pacific (EEP) and the Atlantic has been reconstructed for the time around 4.4 Ma [2,13,14], where diverging planktonic foraminifera $\delta^{18}O$ records from the Caribbean and the Eastern Equatorial Pacific (EEP) show the build-up of the modern Pacific–Caribbean salinity contrast and the emergence of the Western Atlantic Warm Pool (WAWP). These findings are supported by simultaneously increasing foraminiferal Mg/Ca ratios [15], indicating rising temperatures in the Caribbean. At Ocean Drilling Program (ODP) Site 999 (Leg 165, Caribbean Sea, 12.73°N, 78.73°W, 2828 m), which is closer to the former seaway, the strong shift towards higher $\delta^{18}O$ values (SSS) is reflected slightly later, at about 4.2 Ma, while during the same interval the Pacific $\delta^{18}O$ values (ODP Site 851, Leg 138, Equatorial Pacific, 2.77°N, 110.57°W, 3761 m) remain virtually unaffected [13].

The gradual closure of the seaway lead to an intensification of North Atlantic thermohaline circulation (THC) with better ventilated Caribbean deep waters, as suggested by increasing benthic $\delta^{13}C$ values and higher carbonate preservation at ODP Site 999 [9]. Stronger deep water formation in the North Atlantic had to be compensated by a strengthened Gulf Stream, followed by an increase in the northward heat transport. This notion is consistent with results from a sediment record south of Iceland (ODP Site 984, Leg 162, Bjorn Drift, 61.25°N, 24.04°W, 1648 m), where reconstructed sea surface temperatures (SSTs) increase by about 2–3 °C around 2.8 Ma, just prior to the final closure of Panama [16].

The final closure of the gateway around 2.75 Ma, also associated with the exchange of land mammals between North and South America [17], coincides with the intensification of Northern Hemisphere glaciation, evident by the emergence of large amounts of ice-rafted debris (IRD) in North Pacific [18,10] and North Atlantic deep sea sediments [19,16]. In the North Pacific, a sudden drop of opal accumulation rates has been attributed to the onset of the strong present day like stratification [20], which might have triggered glaciation over North America [21]. The following climate of the Pleistocene was characterized by strongly oscillating glacial/interglacial cycles [6].

Changes in gateway configurations, especially the closing Panama seaway, and their relevance for ocean circulation and climate have been subject to several theoretical and modeling studies. Using the theory of 'Island Rule' [22], it was found that with an open Panama Isthmus, a closed Bering Strait and in the absence of North Atlantic Deep Water (NADW) formation the flow through the gateway should be directed from the Atlantic into the Pacific. However, results from different 3-D ocean circulation models found the opposite, with the net transports being directed from the Pacific into the Atlantic, supplying the North Atlantic with low salinity sub-surface water, even in some cases where the surface flow may be (seasonally) in westward direction [23,24,3,26,27].

In most models closing the Panama gateway is associated with a strengthening of the meridional overturning and the western boundary current in the North Atlantic, and these changes seem to depend primarily on the degree of restriction of the throughflow [24,3,26]. In general, the transport of fresh surface and sub-surface waters from the Pacific into the Atlantic causes North Atlantic surface waters to become more buoyant, leading to low NADW formation rates. Nevertheless, even for a deep sill model results of the Atlantic overturning range from a total collapse [23,27] to a transequatorial transport of NADW around 10 Sverdrup (Sv, 1 Sv $=10^6$ m^3 s^{-1}) [25]. Trying to assess threshold values for the total collapse of NADW formation or even the quantification of changes in overturning rates is a problem, as in ocean models these processes are highly sensitive to the parameterization of sub-grid scale processes, like vertical diffusivity K_υ, which is an important but at present weakly constrained parameter [28,29].

Most modeling studies concerned with the Panama closure investigated the effects on the physical climate components whereas effects on the marine ecosystem have not been given much attention. A noticeable exception is the work by Heinze and Crowley [30] who concentrated on the effect of changes in gateway configurations on sedimentation patterns in the ocean. However, no model study has yet examined the impact of ocean circulation changes on nutrient redistributions and resulting marine productivity.

Here we use a global coupled climate–marine ecosystem model to simulate the impact of the closing Panama Isthmus on ocean circulation and, for the first time, on marine biological productivity. Our findings will be compared to results from other model studies and paleo records from deep sea sediments.

2. Model and experiments

The University of Victoria Earth System Climate Model (UVic-ESCM Version 2.6) used in this study is a coarse resolution model of intermediate complexity. The ocean general circulation model is based on MOM-2 [31] with eddy induced tracer mixing parameterized according to Gent and Mc Williams [32], and there is no flux correction applied. The horizontal resolution is 1.8°×3.6° and there are 19 vertical layers of 50–500 m thickness, increasing with depth. Assessing diapycnal mixing is an important but currently not very well resolved factor in ocean modeling [29]. Direct measurements of vertical diffusion (K_υ) show values of about 0.1 $cm^2\ s^{-1}$ in the subtropical pycnocline [33], whereas results from inverse modeling [34] and observations of fluctuations of internal wave velocities in the Southern Ocean [35,36] suggest values of an order of magnitude higher. To address this problem, two different profiles are used for the vertical diffusivity (K_υ) in our study. In the first set of experiments K_υ increases from 0.3 $cm^2\ s^1$ at the surface to about 1.3 $cm^2\ s^{-1}$ at 5000 m depth, while in the second line of experiments K_υ ranges from 0.6 $cm^2\ s^{-1}$ to 1.6 $cm^2\ s^{-1}$ [29].

The ocean circulation model is coupled to a vertically integrated energy–moisture balance model of the atmosphere and to a dynamic–thermodynamic sea ice component [37]. Atmospheric wind velocities used in the momentum transfer to the ocean and sea ice as well as for moisture advection and in the calculation of surface heat fluxes are prescribed using a mean seasonal cycle. Orbital parameters (eccentricity, obliquity and precession), which influence the strength and distribution of incoming solar radiation, are set to present day values. The atmospheric pCO_2 is kept on a constant preindustrial level of 280 ppm. A more detailed description of the model version used in this study is given by Weaver et al. [38].

The ecosystem model used in our study is described in Schmittner et al. [29]. It consists of four prognostic variables: nutrients (N), phytoplankton (P), zooplankton (Z) and detritus (D), based on nitrogen as the exemplary and only limiting nutrient. The model does not account for limitations by other nutrients like iron or phosphorus and neglects nitrogen fixation as well as denitrification.

Four experiments have been carried out with different Panama sill depths to represent several stages in the gradual closure of the seaway, for each of the two diffusivity (K_υ) profiles. In the first experiment, which is the control run for the preindustrial situation, the Panama gateway is closed, while in the other experiments the sill depths are 130 m (shallow), 700 m (intermediate) and 2000 m (deep), respectively. The opening of the Panama gateway extends over two grid boxes (one velocity grid point), which corresponds to about 450 km. After integrating over 2000 yrs, the model is in equilibrium. For a more convenient distinction between the different experiments they will hereafter be named LD, for low vertical diffusivity parameterization (K_υ=0.3–1.3 $cm^2\ s^{-1}$), HD for high vertical diffusivity (K_υ=0.6–1.6 $cm^2\ s^{-1}$), and furthermore they will be assigned the suffixes 'closed', 'shallow', 'intermediate', or 'deep' to indicate the sill depth of the Panama gateway.

3. Results

3.1. Ocean circulation

3.1.1. Barotropic flow

The depth integrated flow, which is mainly driven by wind stress, is similar for both diffusivity setups and each of the Panama sill depths. Noticeable changes associated with the proceeding Panama closure are a weakening of the clockwise gyre circulation in the low latitude Pacific from 15 Sv to 5 Sv. Isolines crossing the Panama seaway indicate net water mass transport from the Pacific into the Atlantic Ocean (not shown). Note that these changes in the barotropic flow are not caused by varying wind stress, which is identical in all simulations. Rather they are a consequence of changes in the baroclinic flow and its interaction with topography (JEBAR effect).

3.1.2. Panama throughflow

As indicated by the barotropic circulation pattern, water mass transports through the gateway are always directed from the Pacific into the Atlantic. These transports are decreasing with shallowing of the sill (Table 1). In total, for the LD experiments the transports decrease from 10.6 Sv (deep) over 10 Sv (intermediate) to 5 Sv (shallow). In the HD experiments the fluxes are generally higher (16–7 Sv), but relative changes are comparable. Although net transports are directed from the Pacific into the Atlantic, seasonal reversals of the flow direction may occur. For example, in the LD experiments, there are seasonal reversals near the surface, with transports during winter and spring directed from the Atlantic into the Pacific (Fig. 1). For the deep opening we find seasonal reversals of deep water exchange (800–2000 m) in the LD experiment. No such reversals are apparent in the HD experiment which simulates permanent outflow of deep water from the Atlantic to the Pacific (Fig. 1), consistent with results from Nisancioglu et al. [25].

The net water mass transport from the Pacific into the Atlantic is maintained by a steric height gradient between the two ocean basins as demonstrated earlier [3] and illustrated in Fig. 2. Steric height in the Eastern Equatorial Pacific is generally higher than in the Western North Atlantic and the gradient increases with proceeding gateway closure, while there are no conderable differences between LD and HD (Table 1). Steeper gradients of steric

Table 1
Panama sill depths for the different experiments as well as results for steric height gradients between different ocean basins, North Atlantic Deep Water (NADW) formation rate and throughflow rates through the gateways of Panama and Indonesia, respectively

Experiment	Sill (m)	Steric height difference			Gateway throughflow	
		Pacific–Atlantic (m)	Pacific–Indian (m)	NADW (Sv)	Panama[a] (Sv)	Indonesia[b] (Sv)
LD_{closed}	0	0.84	0.17	13.3	–	20.1
$LD_{shallow}$	130	0.71	0.15	10.6	5	14.9
$LD_{intermed}$	700	0.57	0.18	4.8	10	8.7
LD_{deep}	2000	0.56	0.18	5.5	10.6	8.0
HD_{closed}	0	0.85	0.19	18.3	–	23.7
$HD_{shallow}$	130	0.70	0.17	16.6	6.9	17.0
$HD_{intermed}$	700	0.57	0.18	13.1	15.8	7.4
HD_{deep}	2000	0.56	0.18	13.4	13.8	7.0

[a] Transport from Pacific into Atlantic.
[b] Transport from Pacific into Indian Ocean.

height lead to higher current velocities through the gateway for shallower sill depths, enabling a throughflow of still 5–7 Sv for a 130 m deep sill. The higher throughflow rates in the HD runs indicate that there is a further influence of the deep water formation rate in the North Atlantic on the throughflow, as the steric height gradients in both lines of experiments are about the same, but as in the HD experiments there is more deep water formation taking place (see results below) this leads to a higher throughflow through the Panama gateway.

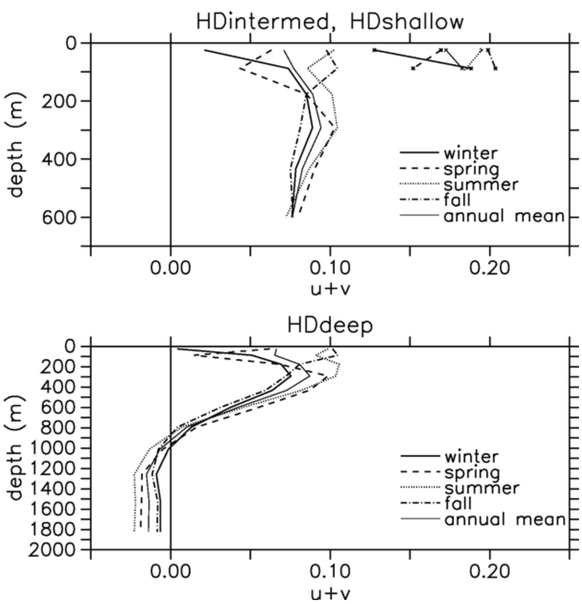

Fig. 1. Annual and seasonal mean profiles of throughflow velocities (m s^{-1}) through the Panama gateway. Top: results for shallow and intermediate sills (HD), bottom: deep sill (HD). Positive (negative) values correspond to flow from (into) the Pacific into (from) the Atlantic.

3.1.3. Atlantic THC

Along with the gradual closure of the Panamanian seaway North Atlantic Deep Water (NADW) formation intensifies in the model (Table 1). The rate of NADW formation is defined as the maximum of the Atlantic meridional overturning stream function below 300 m depth. In the LD experiments NADW formation increases from 5.5 Sv (LD_{deep}) to 13.3 Sv (LD_{closed}). That is, meridional overturning has almost collapsed for the deep and intermediate sill depths and starts to develop from the intermediate sill depth onwards. In the HD setup, on the other hand, there is a considerable amount of deep water formation occurring at all times. Here the rates are increasing from 13.4 Sv for the HD_{deep} experiment to 18.3 Sv for HD_{closed} (Fig. 3 and Table 1). These results clearly show the model sensitivity to vertical diffusion, however, the modern overturning rates in both experiments are within the range of current estimates for the maximum overturning based on models [39] and observations [40,41,34]. An increase of NADW formation following the Panama closure is also consistent with paleo records. Haug and Tiedemann [9] found higher benthic $\delta^{13}C$ values and better carbonate preservation in the Caribbean (ODP Site 999) during the time of the final closure of the gateway (5–2 Ma), indicating stronger ventilation, possibly by more intense formation of upper NADW.

Forced by the increasing thermohaline circulation in the North Atlantic a strengthening of the Gulf Stream and the North Atlantic drift appears in our model, which is in good agreement with earlier modeling studies [3,25,26]. Consequently, after the Panama closure, the modern type of the Gulf stream circulation establishes with stronger surface and sub-surface currents, leading to higher sea surface temperatures (SST) and higher sea surface salinities (SSS) in the North Atlantic (Fig. 4). The maximum warming of 4 K (LD) to 6 K (HD) is found southwest of

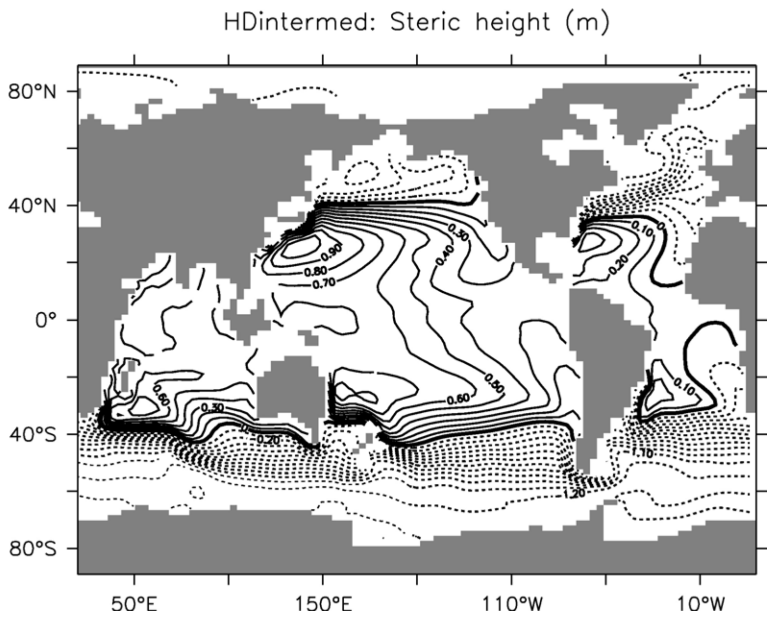

Fig. 2. Steric height (m) for the intermediate Panama sill simulation (HD).

Iceland from the deep to the closed passage runs. An interglacial temperature rise of 2–3 K, as reconstructed from deep sea sediments south of Iceland by Bartoli et al. [16], is in reasonable agreement with the modeled temperature change of 1.7 K (LD) in this area, when changing from intermediate to shallow sill depth. However, for the final closure (moving from shallow to closed sill), there is only a small warming by about 0.3 K

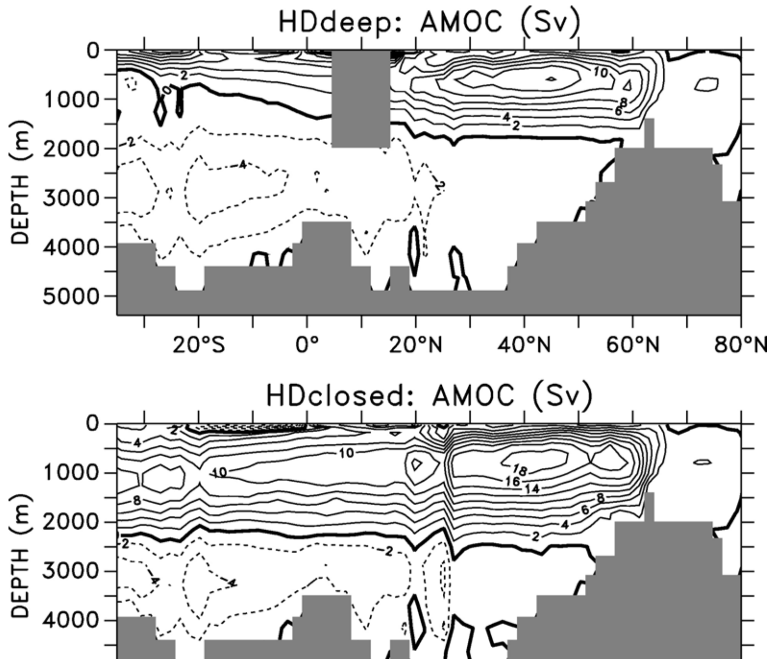

Fig. 3. Atlantic meridional overturning stream function (AMOC) for the experiments HDdeep (top) and the HDclosed (bottom). Solid lines and positive numbers indicate clockwise circulation; dashed lines and negative numbers show counter-clockwise circulation.

(LD). This discrepancy in the timing is further discussed in Section 4. The North Atlantic SST increase is accompanied by rising SSS with a maximum difference between the deep opening and closed sill of about 2 units, located in the central Irminger Sea. At the same time SSTs in the South Atlantic are decreasing by about 2–3 K in concert with a moderate decrease of SSS by 0.5–1.

3.1.4. Indonesian throughflow

Transports through the Indonesian Archipelago are highest for the closed Panama seaway situation (20–24 Sv) and lowest for the deep sills (8–7 Sv), demonstrating an intimate connection between both gateways (Table 1). Minor differences between LD and HD indicate that these results are robust and largely independent of the actual K_v parameterization. The current transport estimates through the archipelago range from 10 Sv (model result, [42]) to 16±5 Sv, obtained by inverse methods [34], i.e. our results for the LD experiments are within the range of other estimates, while the HD experiment seems to overestimate the present day transport. During the closure of Panama, the surface return flow of NADW upwelled in the Pacific can no longer take the shortcut through Panama and now has to embark on a longer journey back into the North Atlantic via the Indonesian Gateway and the Indian Ocean. However, sediment records suggest a lowering of the Indonesian throughflow at the time around 5–3 Ma [43], i.e. prior to the final closure. This is in contrast to our model results, but can be explained by tectonic movements within the Indonesian Archipelago, restricting the throughflow [42], which is not considered in our model framework.

3.2. Nutrients and primary productivity

The fundamental changes in ocean circulation associated to the closing Panama seaway strongly affect nutrient distributions and marine productivity. Particularly at higher latitudes, significant shifts are found with generally decreasing surface nutrient concentrations in the North Atlantic and Arctic Ocean and increasing surface nutrients in the Southern Ocean (Fig. 5). The strongest relative impact takes place in the North Atlantic, north of 40°N, and in the Arctic Ocean, where surface nutrient concentrations are depleted by 30–50% with the transition from the deep/intermediate sill depths to the shallow/closed situation. This is caused by reduced advection of nutrient-

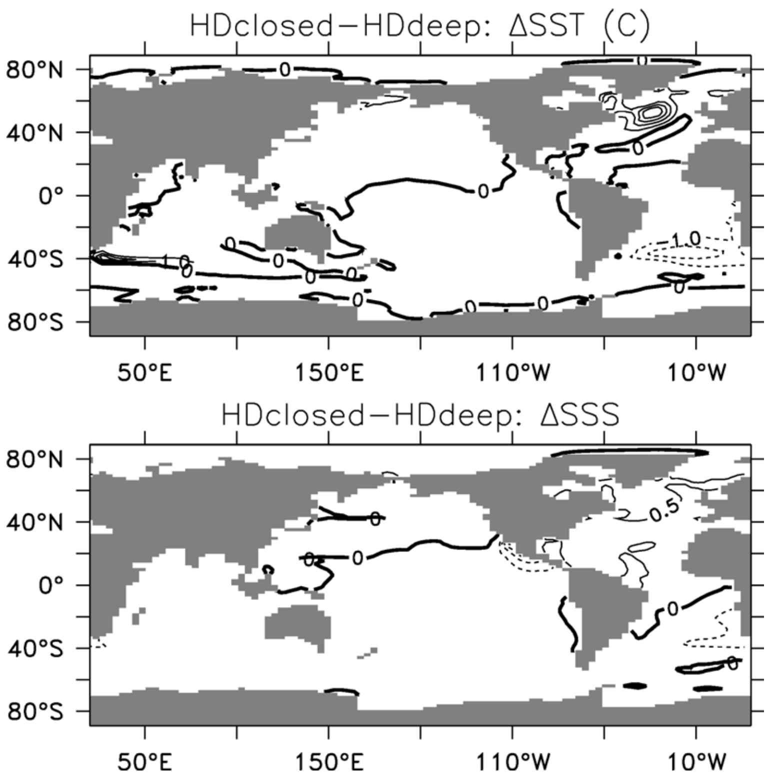

Fig. 4. Differences in SST (top) and SSS (bottom) between the closed and deeply opened Panama gateway simulations (HD). Solid lines and positive numbers indicate increasing temperatures and salinities, dashed lines and negative numbers show decreasing temperatures and salinities. Differences between contour lines are 1 °C (top) and 0.5 °C (bottom).

rich sub-surface waters from the Pacific through the Panama gateway. As shown in Fig. 1, transport rates through Panama are highest in the depth range between 300 and 500 m and even though surface nutrients are very low in the low latitude Pacific there is a steep vertical gradient with nitrate concentrations reaching values of about 20 μmol kg^{-1} at 200 m water depth (not shown). The restriction of nutrient-rich Pacific outflow leads to nutrient depletion in the North Atlantic and Arctic surface waters, which is further amplified by the effect of increasing NADW formation, leaching out nutrients from the Atlantic.

In the Southern Ocean the higher surface nutrient concentrations are coming from deeper layers, which is a result of the more intense thermohaline circulation (THC), a similar effect as described in Schmittner [44]. Local Southern Ocean nutrient stocks respond weakly to the modeled gateway closure (Fig. 5); therefore, higher surface nutrient concentrations reflect further progressive nutrient depletion of deep waters (below 1000 m), which is caused by the injection of low nutrient NADW (not shown).

In the low latitude oceans, where surface water nutrient concentrations are generally low, the influence of the closing gateway is rather small, except for the Eastern Equatorial Pacific (EEP), where restriction of the outflow and slightly stronger upwelling, also a consequence of the Panama closure, strongly increase surface nutrient concentrations (Fig. 5). The amount of upwelling increase is in the order of up to 5 cm day^{-1} for the EEP surface water (upper 50 m), which corresponds well to earlier results from Maier-Reimer et al.

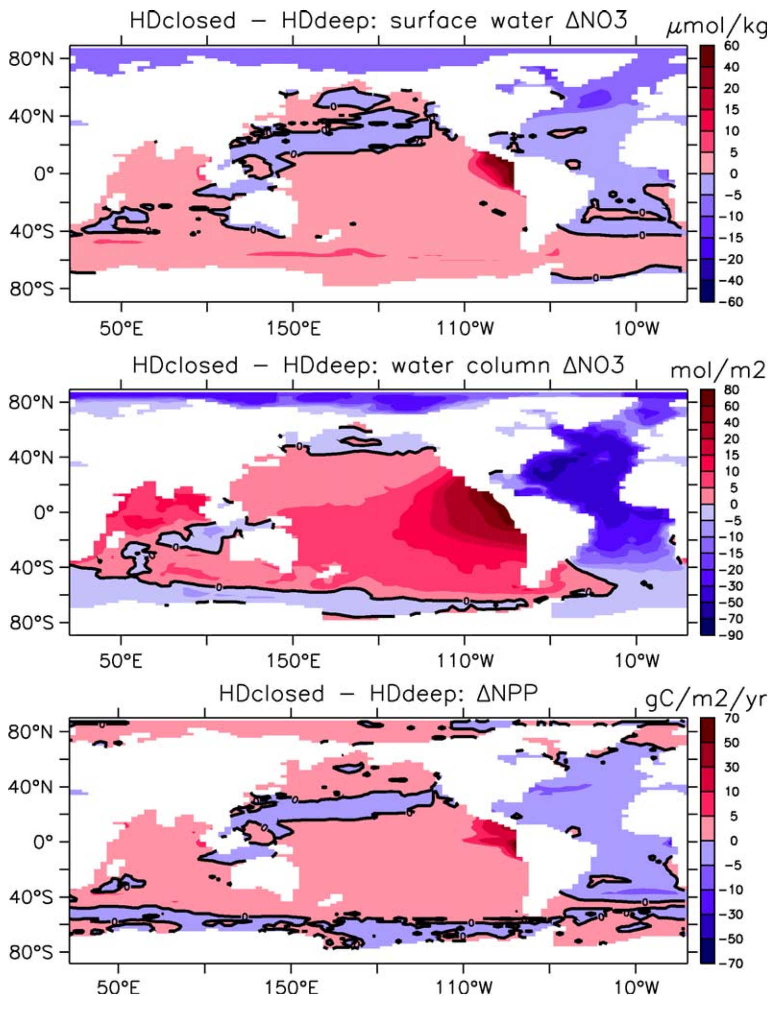

Fig. 5. Differences in nutrient (nitrogen) concentrations and productivity between the closed and deep Panama gateway simulations (HD). Top: difference in surface water (upper 100 m) nutrient concentration, center: difference in vertically integrated nutrient concentrations, bottom: vertical integral of difference in net primary production (NPP).

[23]. Although the amount of this change may be small, on longer time scales even a slight change in the vertical velocity leads to a shallowing of the nutricline.

Depth-integrated nutrient concentrations decrease in the entire Atlantic and Arctic Oceans (Fig. 5), due to decreased import from the Pacific through the Panama gateway and to increased rates of low nutrient NADW formation. The Southern Ocean seems to remain almost unaffected, whereas the nutrient inventory in the Eastern Equatorial Pacific (EEP) is strongly growing in concert with the gradual closure of the Panama gateway. Especially in the HD experiments nutrient stocks are doubling here with closure of the gateway.

The changing nutrient distributions leave their imprint on marine productivity patterns (Fig. 5). Generally, in both diffusivity setups globally integrated NPP is increasing by 20–25% from the deep sill until closure of the seaway (Table 2). This increase is basically consistent with model results of Heinze and Crowley [30], however, absolute rates of NPP are different between the two diffusivity setups. In the LD experiments NPP is significantly lower than in the HD experiments, so that lowest global NPP is found for LD_{deep} and $LD_{intermediate}$ (24 Gt C yr^{-1}), which then increases to a value of about 30 Gt C yr^{-1} in the LD_{closed} experiment. For the HD experiments lowest NPP is also simulated for the deep and intermediate sill depths, but still much higher values of about 45 Gt C yr^{-1} are achieved here, which then increase to 53 Gt C yr^{-1} after closure. Differences between the two diffusivity setups are caused by the shallower nutricline in the HD experiments [29], which makes more nutrients available for production. The general increase of global NPP with closing Panama seaway in both lines of experiments can be explained by intensification of the meridional overturning circulation, which reduces the ocean mixing time and thus accelerates upwelling of nutrient-rich deep waters, which in turn maintains higher productivity at the sea surface [44].

In the North Atlantic, however, NPP does not follow the global trend of increasing productivity with proceeding Panama closure. Here, between 30° and 60°N, NPP is decreasing by about 30% from the deep to the closed sill for both diffusivities (Table 2), caused by the depletion of nutrient stocks due to the Panama closure (Fig. 5). Especially in the HD experiment there is a pronounced drop in the North Atlantic NPP related to the final closure. The results are consistent with a change in the benthic foraminifera species assemblage at ODP Site 984 (south of Iceland), indicating a switch in the dominating species from a high to a low productive species around (2.75 Ma) the time of the final closure [16]. However, we cannot exclude that the observed productivity drop was caused by a different process, like e.g. the onset of the ice ages.

Table 2
Model results of integrated net primary production (NPP)

Experiment	Global (Gt C yr^{-1})	N-Atlantic[a] (Gt C yr^{-1})	EEP[b] (Gt C yr^{-1})	N-Pacific[c] (Gt C yr^{-1})
LD_{closed}	30.5	2.4	3.8	3.5
$LD_{shallow}$	28.2	2.8	2.7	3.7
$LD_{intermed}$	23.9	3.3	1.0	2.8
LD_{deep}	24.0	3.3	1.1	2.8
HD_{closed}	53.3	3.4	8.7	5.4
$HD_{shalllow}$	48.7	5.0	5.0	5.5
$HD_{intermed}$	44.6	5.3	2.3	5.0
HD_{deep}	45.0	5.2	2.4	5.2

[a] 30°–60°N.
[b] 20°S–30°N, 110°–70°W.
[c] 30°–65°N.

Further discussion of the productivity changes, in particular with regard to the timing, is provided in Section 4.

In the North Pacific, north of 30°N, there is a 30% increase of NPP from the deep to the shallow sill in the LD experiments, but then NPP is slightly decreasing again (Table 2). For the same time in the HD experiments, there are only minor variations of ±6% for NPP at different sill depths. Sediment records [20] show a gradual increase in opal accumulation rates from 6 to 3 Ma BP, not inconsistent with the simulated increase in productivity. However, the sharp drop in the observations at the time of the final closure cannot be reproduced by the model. This drop is generally interpreted as a reduction of marine productivity at that time [20] associated with the development of a strong halocline after the Panama closure. One possible reason for this discrepancy is the neglect of changes in Bering Strait throughflow in our simulations. Reduced flow of fresh North Pacific waters through Bering Strait into the Arctic in response to sea level lowering after the onset of glaciation would have increased stratification in the North Pacific.

In our model simulations, the strongest regional impact of the closing Panama seaway on NPP is found in the Equatorial East Pacific (EEP), where the model results show a more than 3-fold increase from the deep sill to closed Panama for both diffusivities. This result is consistent with sediment records, which show an eastward shift in the maximum of $CaCO_3$ accumulation rates from 100° and 110°W around 6 Ma towards the South American continent between 80° and 90°W around 3 Ma [45] as well as a similar shift in opal accumulation [46]. At the same time, a clear drop in the $\delta^{13}C$ values of benthic foraminifera from ODP Site 677 (Leg 111, Panama Basin, 1°N, 84°W, 3461 m) [47] indicates higher nutrient concentrations in the bottom water. These higher nutrient concentrations in the deep Panama basin may be caused by two factors, accumulation of nutrients due to the gradual gateway closure on the one hand (Fig. 5) and enhanced flux of organic material on the other hand, delivering $\delta^{13}C$ depleted material to the sea floor. Increased productivity, sinking and remineralization of organic matter would also have led to the intensification of the oxygen minimum zones and hence denitrification. This negative feedback, which is not included in the model, would have muted the EEP productivity increase in the real world.

Taken together, the modeled effects of the Panama closure on nutrient distributions and marine productivity are largely consistent with sediment records. Especially a pronounced drop in the North Atlantic NPP can be supported by a change in species compositions, indicating a switch from high to low productive species at the time of the final closure [16]. Furthermore, a massive NPP increase in the Eastern Equatorial Pacific (EEP) correlates very well with increasing and eastward shifting mass accumulation rates of $CaCO_3$ [45] and opal [46], as well as with decreasing ^{13}C from benthic foraminifera in the Panama basin (ODP Site 677) [47].

4. Discussion

Clearly, the closure of the Panama gateway resulted in the establishment of the modern ocean circulation pattern. Intensified thermohaline circulation (THC) is caused by reduced inflow of fresh surface water from the Pacific into the Atlantic and further advection to the North Atlantic areas of deep water formation. Increased densities in the North Atlantic strengthen the meridional gradient in depth-integrated steric height (Fig. 2), thereby accelerating the meridional overturning. However, quantitatively large differences are found for different values of vertical diffusivity (K_υ) in the model. Particularly, the simulations with intermediate and deep (700 and 2000 m) sill depth show a collapsed overturning for the weak mixing case (LD), whereas in the high mixing case (HD) still a considerable amount of NADW is produced. These differences might also explain discrepancies between different models [24,3,25,26,23,27]. As there is lingering disagreement about the quantification of K_υ [33–36], judgment of the different simulations might be aided by a comparison with the paleo proxy record.

The first appearance of NADW, or an early precursor of it, is determined by seismic stratigraphy analysis for the early Oligocene, at about 35 Ma [48]. This finding replaces results from earlier studies, which scheduled the onset of NADW formation for the Miocene or Pliocene, however, it merely describes the existence of a southward directed deep water current in the North Atlantic, rather than its strength and climatic relevance. Wright and Miller [12] found a correlation between mantle plume activity at the Greenland–Scotland–Ridge and the production of Northern Component Water (NCW), which first occurred at about 17 Ma and is the source of NADW. In their study, high tectonic activity is associated with a shoaling of the ridge and thus ceasing NCW formation, while less activity permitted NCW formation to recover. However, they concluded that tectonic activity has not triggered the long-term climate trend during Neogene, but certain Miocene and Pliocene climatic optima and coolings seem to be amplified by the ridge activity.

Assessment of the Neogene evolution of the strength of Atlantic THC and its variability in the current literature reveals sometimes conflicting results based on different paleo proxy records. A succinct overview is given by Frank et al. [49]. Generally, $\delta^{13}C$ from benthic foraminifera which is used to infer changes in ocean ventilation rates from nutrient concentrations (high $\delta^{13}C$=low nutrient concentration=good ventilation), shows an increase in NADW formation with the gradual Panama closure. For example, Bickert et al. [50] found the deep Atlantic Ocean to be well ventilated as early as 8 Ma ago and Haug and Tiedemann [9] determined higher $\delta^{13}C$ ratios accompanied by better carbonate preservation in Caribbean sediments (ODP Site 999) for the time around the final closure (5–3 Ma), indicating better ventilation, as already mentioned above. On longer time scales, Frank et al. [49] determined from Nd and Pb isotopes of ferromanganese crusts, that during the last 14 Ma there was a considerable amount of NADW formation constantly taking place, which, since the onset of Northern Hemisphere glaciation (NHG) at about 3 Ma, progressively decreased. The decrease is quantified in the order of magnitude of 14–37%, when comparing NADW formation at 3.5 Ma with the present (interglacial) value. However, as the growth of ferromanganese crusts is very slow, in the order of a few millimeters per Ma, their temporal resolution is low. Especially for the time interval from 3 Ma, when glacial periods prevailed, the results of Frank et al. [49] may be biased towards glacial conditions, which can explain the tendency to obtain lower ventilation rates from these records.

The discussion shows that a straightforward determination of the total amount of NADW formation and its variability can neither be obtained by paleo records nor by climate models alone. Therefore, to achieve a better quantitative estimate, an approach linking both models and observations should be pursued. As a first step, we correlate modeled and observed $\delta^{13}C$ distributions, which should allow to find the model solution which is in best agreement with proxy records. For the modeled $\delta^{13}C$ values we use a linear relationship of nutrient concentrations versus $\delta^{13}C$, which is determined from modern data (WOCE, http://www.ewoce.org), as $\delta^{13}C = 0.05 \cdot NO_3 + 2.13$, and assume this relation to be valid also for the Pliocene. Note that changes in fractionation due to air–sea gas exchange are neglected in this approach.

The so obtained model $\delta^{13}C$ values (Fig. 6) are compared with the results from Ravelo and Andreasen [5], who determined meridional transects of $\delta^{13}C$ from the Atlantic and the Pacific for recent values and the early Pliocene (3.1–4.4 Ma). Using model-derived $\delta^{13}C$ values from locations of 11 sediment cores we find that the best agreement, i.e. highest correlation coefficient ($R=0.926$) and lowest rms-pattern error (rmsp = 0.38), for modern $\delta^{13}C$ is obtained for the HD_{closed} experiment. This indicates that among the model setups used here the HD parameterization seems to represent the modern circulation pattern better than using LD. However, for the early Pliocene sediment $\delta^{13}C$ values, we also find the best correlation with HD_{closed} ($R=0.829$). This result indicates that the early Pliocene Atlantic meridional overturning circulation was not weaker than it is today and is not inconsistent with the conclusion of Ravelo and Andreasen [5] that it was even stronger than today. An incongruity seems to exist between this conclusion and the assertions made above after which the simulated effect of the final closure on ocean circulation, SSTs and productivity in the North Atlantic seem to be consistent with the observations from Bartoli et al. [16].

The most likely explanation of this discrepancy is related to model resolution and gateway aperture. Geologic reconstructions suggest a complex topography of the seaway with possibly several narrow openings and the appearance of islands [51]. Due to the coarse resolution of the model the gateway is oversimplified and probably too wide. It is therefore likely that the throughflow in the real world was much more restricted than simulated by the model. Our shallow sill simulations therefore are probably more representative of a time period distinctly earlier than about 4–3 Ma BP. Consequently, in our shallow sill experiments the throughflow and hence the influence of low salinity surface and sub-surface waters advection from the Pacific on NADW formation is probably overestimated. Thus, it seems possible that the observations from the North Atlantic during the final closure from 3.3 to 2.5 Ma [16], i.e. a transient, step-wise interglacial warming and the decrease of productivity, might either not be caused by a change of the Panamanian throughflow or that the throughflow restrictions were reversible and not monotonous. Irrespective, the mechanism causing the intensified circulation during the early Pliocene as found by Ravelo

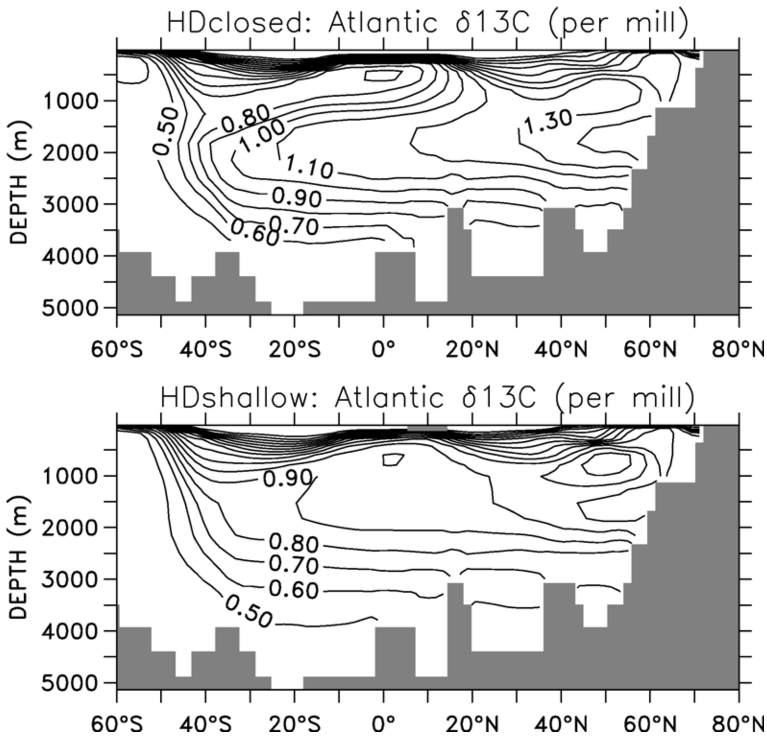

Fig. 6. Model-derived $\delta^{13}C$ cross sections through the Atlantic Ocean along 25°W from the HD experiments for the modern situation (top) and the shallow sill (bottom).

and Andreasen [5] remains unknown and is not considered in our model framework. An alternative, but maybe less likely, explanation of the above mentioned incongruity might be that the circulation was strong during the early Pliocene despite considerable throughflow through Panama and that it even further intensified during the final gateway closure, causing the observed warming and productivity decrease observed in the North Atlantic.

Modeled changes in marine nutrient concentrations caused by the closure of the Panama gateway are also largely consistent with sediment records, especially the pronounced drop of North Atlantic NPP at the transition from shallow to closed sill in the HD experiments, corresponds very well to a record of a change in species composition of benthic foraminifera towards a lower productive species [16]. In the eastern equatorial Pacific increased productivity from our model results is supported by sediment records showing higher mass accumulation rates of $CaCO_3$ [45] and opal [46], as well as by decreasing $\delta^{13}C$ from benthic foraminifera [47]. Whereas in the subarctic North Pacific results from our model experiments and sediment records diverge. While the model simulates a slight increase in productivity, there is a pronounced drop in opal mass accumulation rates around the time of the final Panama closure in the observations [20]. There may have been, however, other circulation-driven changes involved leading to the observed changes in sedimentation/accumulation patterns. For example, the drop in opal accumulation might be related to higher iron input into the North Pacific, which is reported to have started to increase as early as 3.6 Ma ago [52], and which may have lead to a change in the silicon to nitrogen uptake ratios of marine plankton. Generally, the molar Si/N uptake ratio of diatoms is about 4 : 1 under iron limitation and shifts towards 1 : 1 when iron is replete [53,54]. Consequently, higher iron deposition, as it is expected to have occurred in the North Pacific after the onset of NHG, may have changed the Si/N uptake ratios, requiring more nitrogen per mol silicon which is taken up by diatoms. This includes that diatom cells are less silicified and thus not as heavy as before and probably more prone to dissolution. This theory is consistent with sediment records showing decreasing silicon isotope values [55] with increasing $\delta^{15}N$ values (ODP Site 882, Leg 145, Subarctic Northwest Pacific, 50.35°N, 167.58°E, 3244 m) at the time of the drop in opal accumulation rates [20]. If only productivity had decreased in general, both isotope ratios should have changed into the same direction, i.e. both should have become lower. This oppositional behavior, however, indicates that there was probably a shift from a silicon and/or iron limited production prior to the NHG (and Panama closure, respectively) towards a nitrogen limited system during the glacial period (after Panama closure, respectively). The emergence of nitrogen limitation was furthermore supported by higher silicate and lower nitrogen advection from the sub Antarctic into the North Pacific during glacials than during interglacials [54], so that in total North Pacific marine productivity may have decreased, although 'iron fertilization' took place. In summary, the changes in nutrient cycling, which may have caused the drop in opal accumulation rates in the North Pacific (ODP Site 882) are not necessarily directly related to the closure of the Panama Gateway. But if the closing gateway caused the onset of NHG, this might have caused increased stratification and lower opal accumulation.

The role of changes in ocean circulation caused by the closure of the Panama gateway on the intensification of Northern Hemisphere glaciation (NHG) is still not clear, yet the temporal coincidence remains striking. From our results, it seems that important changes in ocean circulation can already be found at the transition from intermediate to shallow sill and further on from shallow sill to the complete closure. Especially for the LD experiments considerable deep water formation in the North Atlantic does not start until there is a shallow sill at the Panama gateway, which is far before NHG. Similar as in Klocker et al. [56] we found that after closure of the Panama gateway stronger northward heat and moisture transports indeed leads to higher precipitation, also as snow, over Greenland, which would support an intensification of the NHG. Nevertheless, we can not find significant differences in the extension of the Greenland ice sheet neither between different gateway configurations nor different diffusivity setups. Furthermore, the effects of increased deep water formation and higher marine NPP which are both assumed to lead to stronger CO_2-drawdown from the atmosphere into the ocean, turn out to have only a minor impact on the atmospheric pCO_2 as indicated by simulations with the same model but including the marine carbon cycle (unpublished results). Therefore, from our model results, the hypothesis of the closure of the Panama gateway as a major mechanism for the intensification of NHG cannot be confirmed. There may however, be some drawbacks in the application of a seasonally prescribed energy–moisture balance model of the atmosphere, which is probably not suitable to capture delicate changes in the balance of snow accumulation/glacier melt at high latitudes, which in turn is an important mechanism deciding whether an ice sheet builds up or not.

We can conclude that the Panama closure induced changes in ocean circulation that supported, but obviously did not finally cause the intensification of the NHG around 2.75 Ma. Probably, a sum of different factors including ocean circulation changes [23,24,3,25–27], changing precipitation patterns in high latitudes [10,56,21], CO2 drawdown from increased marine productivity, CO_2 drawdown from increased mineral rock weathering [57,58] in conjunction with favorable orbital conditions [9,59] lead to the final switch to glacial/interglacial cycles.

5. Conclusions

- Gateway configurations have a strong impact on ocean circulation, particularly the closure of the Panamanian seaway caused fundamental changes, leading to the build up of the modern type conveyor belt circulation pattern.
- Restriction of relatively fresh upper ocean flow from the Pacific into the Atlantic increases NADW production and the Indonesian Throughflow. However, model results for changes in NADW formation rates show large discrepancies depending on the model configuration.
- Surface velocities through the gateway increase with shallowing sill depth due to increasing steric height differences between the Atlantic and the Pacific.
- Assessing the strength and variability of the (paleo-) THC is not a trivial task as model results depend on the parameterization of sometimes only weakly constrained parameters like, e.g. K_v and sediment $\delta^{13}C$ records, are perturbed by global signals. We show that linking $\delta^{13}C$ records and model simulated $\delta^{13}C$ patterns is a promising approach to assess circulation changes.
- Changes in nutrient distributions associated to reorganizations of ocean circulation lead to shifts in productivity patterns, which are recorded in deep sea sediments from the North Atlantic and the Eastern Equatorial Pacific (EEP): reduced inflow of high nutrient sub-surface water from the Pacific decreased productivity in the Atlantic while in the EEP productivity strongly increased.

Acknowledgments

We would like to thank Peggy Delaney and two anonymous reviewers for their very helpful comments on an earlier version of this manuscript. This work was supported by the Deutsche Forschungsgemeinschaft (DFG) within the Research Unit 451 'Ocean Gateways'.

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