Journal of Experimental Marine Biology and Ecology xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Marine reptiles, birds and mammals and nutrient transfers among the seas and the land: An appraisal of current knowledge

Brian Moss

School of Environmental Sciences, University of Liverpool, Liverpool L69 3GS, UK

ARTICLE INFO

Available online xxxx

Keywords:
Turtle
Whale
Seabird
Coastal
Ocean

ABSTRACT

There is convincing evidence that large land mammals were formerly responsible for substantial transfers of nutrients across the freshwater and land system. Many of them were made extinct, probably by human hunting, around 10 000 to 14 000 BP, and the populations of the survivors were severely reduced as the Holocene progressed. Evidence is examined that such transfers were equally important among the oceans, coastal waters and inland systems as a result of the activities of anadromous fishes, marine reptiles, seabirds and marine mammals. Numbers of all of these have also been greatly reduced as a result of human activities, though largely in the past few hundred years. Their past and present status and potentialities for nutrient recycling and transfers are assessed. Large marine animals have potentially substantial top-down effects in structuring marine communities, though there is good evidence only for sea turtles and inshore habitats. There are many potential pathways for nutrient transfer, reflected in large accumulations on land of guano from seabirds. Great whales, because of their size and movement range, also offer large potentialities for transfer of nutrients across the oceans and from deep water towards the surface. However, from the very limited evidence available, it appears that the absolute global effects of these are likely to have been and to be minor. Transfers on land benefited from large nutrient supplies available in soils, from high productivity arising from light availability, from a dense and diverse mammal community and from a much smaller ratio of freshwater volume to land area. The huge volume of ocean water, its much greater mixing by wind and currents, and lower overall productivity preclude against globally significant changes in nutrient concentrations as a result of the movements of large animals, despite sometimes dramatic local effects of seabirds nesting on land and anadromous fish moving from the ocean to their freshwater spawning grounds. The intense scientific interest in these models, and the supportive vocabulary created to describe these processes, may have led to an overemphasis of their global significance.

Contents

1. Introduction . . . 0
2. Mammals, birds and transfers of nutrients between the freshwater system and the land . . . 0
3. Marine habitats. . . . 0
4. Land/ocean differences . . . 0
5. Potentially important marine vertebrates and their current status . . . 0
6. Seabirds . . . 0
7. Mammals . . . 0
8. Global concepts of conservation and perceptions of the importance of processes . . . 0
9. Transfers among the freshwater system, estuaries and marine waters . . . 0
10. Transfers along the coastal zone and to deeper waters. . . . 0
11. Transfers between the deep ocean and the land . . . 0
12. Transfers within and across oceans . . . 0
13. Conclusions . . . 0
Disclosures . . . 0
References . . . 0

E-mail address: brmoss@liverpool.ac.uk.

http://dx.doi.org/10.1016/j.jembe.2017.01.018
0022-0981/

Please cite this article as: Moss, B., Marine reptiles, birds and mammals and nutrient transfers among the seas and the land: An appraisal of current knowledge, J. Exp. Mar. Biol. Ecol. (2017), http://dx.doi.org/10.1016/j.jembe.2017.01.018

1. Introduction

> *…our concept of what is natural today is based on personal experience at the expense of historical perspective. Thus, "natural" means the way things were when we first saw them or exploited them, and "unnatural" means all subsequent change. As in Magritte's masterpiece,* La Condition Humaine, *we see the world through a model of our own creation that organizes and filters understanding. In the present context, that filter is the sum total of anthropogenic change that took place in the oceans before we were born.* Jackson (2001)

Vertebrates are generally in decline on Earth. One in four species of mammal is threatened with extinction and the numbers of half of the species are declining (Schipper et al., 2008). Sometimes the main declines were early in the Holocene, for example of large land mammals, some of which were made extinct by intensive hunting, possibly linked with small climate changes. For large marine mammals, the decline was probably much later and coincided with organised whaling and sealing (McCauley et al., 2015) and though it has been devastating in terms of numbers, it has been less severe in terms of habitat destruction and permanent restriction of ranges than on land. Threat levels, nonetheless, are considered often to be higher than on land owing to accidental mortality and pollution, and peak in the northern oceans where human influence is the greatest (Schipper et al., 2008). Among other large animals, the remaining marine or semi-marine crocodilians have been actively culled because of perceptions that they are hazardous, and for leather. Persecution for eggs and meat has led to loss of turtles. All but one of seven sea turtle species is now very scarce. Total numbers may be fewer than ten thousand, whereas there were 16–33 million in the Caribbean alone three hundred years ago (Jackson et al., 2001). Of the flatback, green, hawksbill, Kemp's ridley, leatherback, loggerhead, and olive ridley, all but the flatback is listed as endangered or threatened. The situation regarding sea snakes is largely unknown. Seabirds are also highly vulnerable, particularly to by-catching in gill net fisheries.

Nutrients, particularly phosphorus, nitrogen and iron, figure prominently in any discussion of aquatic productivity, either in fresh or salt water. Phosphorus is naturally scarce in relation to need; nitrogen availability depends on bacterial processes that as readily convert it back to the largely unusable form of nitrogen gas as fix it from the atmosphere; and iron is readily precipitated under oxic conditions, despite being globally very abundant. Natural ecosystems on land are highly retentive of nutrients, but to a large extent in freshwaters, and often in coastal marine waters, phosphorus and nitrogen have been mobilised by destruction of natural land ecosystems and replacement by leaky agricultural systems so that problems of eutrophication are extensive. Our insights have been largely determined by recent artificial eutrophication, but recognition that definition of former reference states is important for current management has raised interest in the roles that large vertebrates might have had before their numbers were reduced so greatly, and the possibility that nutrients were then more readily available, to freshwater systems at least.

Because they often range extensively, large vertebrates are potentially capable of transferring large quantities of nutrients over large areas. Movements and migrations appear to have been very important in short-circuiting transfers of nutrients from the land into freshwaters, and from rivers and floodplains back to terrestrial systems (Moss, 2015; Bishop et al., in this issue). Energy in the form of carbon compounds has been similarly redistributed. Parallel linkages between the freshwater/land system with marine systems through intertidal zones and estuaries have been less-well investigated and potential movements across oceans and from deeper to shallower water have been barely contemplated. This review assesses the potential present and former importance of such marine links in the light of changing populations and communities of the more prominent marine and marine-associated vertebrates, other than specifically marine fishes. A summary of recent findings in the terrestrial/freshwater system is first given to set the scene, and then the relevant biology of large marine animals is surveyed and particular aspects of marine nutrient transfers are considered. Large and predatory fish are equally likely to be important in transfers across the oceans and their populations too have been seriously curbed, but the review concentrates on reptiles, birds and mammals because the emphasis is mostly on linkages with the freshwater and terrestrial systems that figure in the life histories of most of the members of these groups. Whales are included, despite no land linkages. Their often very large size and range suggests potentialities for extensive nutrient transfers. Common names are used throughout because these are familiarly used for vertebrates, even in professional discussions, but Table 1 gives scientific names for these.

2. Mammals, birds and transfers of nutrients between the freshwater system and the land

Undisturbed floodplain lakes in the tropics often show characteristics deemed to be undesirable in temperate regions. The may have turbid water from suspended sediment or algae, cyanobacterial blooms, few or no submerged plants and dominance of floating plants, like water lettuce (*Pistia stratiotes*) or water hyacinth (*Eichhornia crassipes*), at their sheltered edges (Fig. 1). These are sometimes perceived as symptoms of eutrophication from human activities, as they would be in temperate regions, but they are found in floodplain lakes that are remote, in catchments that retain native vegetation, and in which there is neither settlement nor farming. They are naturally eutrophic from the movements of large mammals, including hippopotami, elephant, buffalo, zebra, giraffe and antelopes in Africa, capybara, coypu, and swamp deer in South America, and kangaroos and various feral mammals like water buffalo and dromedary in Australia. These animals graze in the catchment and fertilise the lakes with their urine and dung when they come to drink, roll in mud to remove parasites, rest during the daytime or, in the case of predators such as lions, jaguar, caimans and crocodilians, kill land animals and introduce nutrients to the water in the carcass remains (Moss, 2015). Birds may also transfer large quantities of nutrients to lakes where they roost, and such lakes may be called guanotrophic (Choy et al., 2010; Hahn et al., 2007; Hobara et al., 2001; Kitchell et al., 1999; Manny et al., 1994; Moss and Leah, 1982), though in some of these cases the bird populations have been increased owing to human activities such as the siting of landfills, creation of protected areas, and artificial feeding.

Palaeolimnological evidence suggests that freshwater lakes in the temperate zone were much more nutrient-rich early in their history, after their formation when the ice retreated at the beginning of the Holocene. The evidence comes from changes in diatom communities (see Moss (2015) for detailed references) and from concentrations of ^{15}N, which is considered to be a proxy for combined nitrogen in circulation. A world-wide meta-analysis of 86 cores has shown very high levels of ^{15}N at the start of the Holocene, then a decline until about 6000 years ago when levels began to rise again (McLauchlan et al., 2013). Nitrogen levels have risen in the past century or so, from the products of the Haber-Bosch process, but the recent response in ^{15}N has been flat and concentrations have still not attained their concentrations in the early Holocene. This early eutrophic state has been attributed to a richness of fresh rock debris in the catchments as the glaciers retreated, but as the debris was leached out, fertility is believed to have declined and the lakes naturally became more oligotrophic (see Moss, 2015 for detailed references) until their catchments were cleared of natural vegetation and subsequently settled, farmed and fertilised. However, it is now clear that populations of large mammals were abundant on all the continents at the start of the Holocene and it is suggested that their activities short-circuited the nutrient retention properties of natural vegetation and supplemented the supplies of nutrients provided by the rock debris.

Please cite this article as: Moss, B., Marine reptiles, birds and mammals and nutrient transfers among the seas and the land: An appraisal of current knowledge, J. Exp. Mar. Biol. Ecol. (2017), http://dx.doi.org/10.1016/j.jembe.2017.01.018