**Biogeosciences
Discussions**

Can whales mix the ocean?

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Abstract

Ocean mixing influences global climate and enhances primary productivity by transporting nutrient rich water into the euphotic zone. The contribution of the swimming biosphere to diapycnal mixing in the ocean has been hypothesised to occur on scales similar to that of tides or winds, however, the extent to which this contributes to nutrient transport and stimulates primary productivity has not been explored. Here, we introduce a novel method to estimate the diapycnal diffusivity that occurs as a result of a sperm whale swimming through a pycnocline. Nutrient profiles from the Hawaiian Ocean are used to further estimate the amount of nitrogen transported into the euphotic zone and the primary productivity stimulated as a result. We estimate that the 80 sperm whales that travel through an area of 10^4 km^2 surrounding Hawaii increase diapycnal diffusivity by 10^{-6} m^2 s^{-1} which results in the flux of 10^5 kg of nitrogen into the euphotic zone each year. This nitrogen input subsequently stimulates 6×10^5 kg of carbon per year. The nutrient input of swimming sperm whales is modest compared to dominant modes of nutrient transport such as nitrogen fixation but occurs more consistently and thus may provide the nutrients necessary to enable phytoplankton growth and survival in the absence of other seasonal and daily nutrient inputs.

1 Introduction

Diapycnal mixing plays a key role in a wide range of oceanic processes. Mixing is crucial for meridional overturning circulation which shapes our global climate by enabling the poleward transport of energy in the form of heat (Munk and Wunsch, 1998). Meridional overturning circulation determines the extent of contact between oceanic deep water and the atmosphere and this in turn influences the flux of CO_2 between the ocean and the atmosphere. Without diapycnal mixing to overcome ocean stratification, the ocean would turn to a pool of stagnant water within a few thousand years (Munk and Wunsch, 1998). Climate models are thus very sensitive to the influence of

diapycnal mixing yet this remains one of the least understood parameters in climate models (Dalan et al., 2005). Climate change is expected to increase stratification, and so depress diapycnal mixing, in the ocean (Sarmiento et al., 1998) and for this reason it is increasingly important to understand the sources, magnitude and effects of diapycnal mixing.

Diapycnal mixing also exerts local effects on marine ecosystems. Diapycnal mixing transports nutrients from the nutrient-rich deep ocean into the nutrient-limited euphotic zone and thereby stimulates the phytoplankton blooms that form the basis of marine food webs. Diapycnal mixing influences fisheries productivity because the large plankton that are crucial for channelling nutrients into the pelagic food webs proliferate in episodic turbulent environments where high nutrient levels in the water allow a selective advantage for their large cell size (Kiorboe, 1993; Margalef, 1997). Large plankton increase fisheries productivity by uncoupling the microbial loop and channelling nutrients into pelagic food chains (Alcaraz, 1997; Kiorboe, 1993). The magnitude of fish production is thus often related more to the frequency of diapycnal mixing, than to the overall primary productivity (Kiorboe, 1993).

2 Biomixing

The amount of energy needed to mix the ocean at observed levels is approximately 2.9 TW (Dewar et al., 2006). Winds and tides contribute approximately 1 TW each to global mixing (Dewar et al., 2006). The difference between the contribution of winds and tides and the overall amount of energy required is thus approximately 1 TW. This difference was long overlooked as the result of large geographical variations that are averaged in global calculations, however, some researchers have recently suggested that this energy budget imbalance may be a real effect, and that the action of swimming marine organisms may exert enough energy to contribute significantly to ocean mixing (Dewar et al., 2006). If this hypothesis is correct then wind, tides and swimming marine animals each contribute equally to global mixing.

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Biomixing is the term given to describe the action of organisms swimming through the pycnocline and thereby mixing nutrient rich water into the euphotic zone. Initially considered to be negligible (Munk, 1966), biomixing was revisited by Huntley and Zhou (2004) who estimated kinetic energy production on the order of 10^{-5} W kg^{-1} for animals ranging from krill to whales. Subsequent theoretical estimates suggest that the marine biosphere may contribute on the order of 1 TW to oceanic mixing (Dewar et al., 2006). Direct measurements of turbulence behind a krill swarm have confirmed an increase in turbulence on the order of 2–3 orders of magnitude compared to background levels (Kunze et al., 2006).

Debate within the literature has since centred on whether kinetic energy imparted by the biosphere translates effectively into mixing. The mixing efficiency of the biosphere was examined at buoyancy length scales of 3 to 10 m and found to be low (Visser, 2007). The mechanical energy imparted to the ocean by small animals was found to be dissipated almost immediately in the form of heat, and mixing efficiencies only approached maximum levels in larger fish and marine mammals (Visser, 2007). It was argued that the relatively low abundance of these large animals was thought to make their contribution to oceanic mixing negligible (Visser, 2007).

Darwinian mixing, the mixing that occurs when an object moves thorough a body of water and entrains some of the fluid along with it, was examined recently and shown to be effective in small organisms, which comprise the majority of the ocean biosphere (Katija and Dabiri, 2009). However, the passive particle that was used to illustrate Darwinian mixing by Katija and Dabiri (2009) was later criticized for significantly overestimating the mixing effect (Subramaian, 2010) because wakes associated with passive particles are substantially different to wakes behind an actively swimming particle (Subramanian, 2010). Subramanian (2010) concluded that only large animals are able to significantly influence diapycnal mixing and that a methodology for estimating their diapycnal diffusivity must go beyond examining them as a stationary particle and encompass the fact that they are actively swimming while moving through the pycnocline.

Here we present a novel methodology for examining the diapycnal diffusivity that occurs as an adult sperm whale ascends or descends through a pycnocline. To examine the regional influence of this diapycnal diffusivity, we use publicly available nutrient profiles in the Hawaiian ocean (Karl et al., 2001) to estimate the flux of nitrogen that is moved into the euphotic zone by the resident populations of sperm whales (Whitehead, 2002). The Redfield ratio (Redfield, 1934) is used to estimate the primary productivity that is stimulated as a result of the nitrogen input. In light of the knowledge that fisheries productivity is influenced more by the frequency of mixing than the overall primary productivity (Kiorboe, 1993), we compare the frequency with which whales mix nutrients into the photic zone against other dominant modes of nitrogen transport into the surface waters of Hawaii.

3   Study area and species

We consider the population of 80 sperm whales (*Physeter macrocephalus*) that inhabit the waters surrounding Hawaii (Whitehead, 2002). Whales cannot influence mixing in areas where they are absent, thus we wish to estimate the area of water that the whales travel through and upon which they are able to influence mixing (termed the "whale path"). We estimate this by multiplying the horizontal distance travelled by each sperm whale by the width of its turbulent wake. Sperm whales travel at $1.54 \, \mathrm{m \, s^{-1}}$ (Miller et al., 2004) and complete one dive cycle every 67 min, consisting of 50 min diving and 17 min socialising at the surface (Whitehead, 2003). Within the 67 min dive cycle, 25 min is spent travelling horizontally at the bottom of the dive (Whitehead, 2003). We thus estimate that each sperm whale travels a horizontal distance of 2.3×10^3 m per dive cycle ($25 \, \mathrm{min} \times 1.54 \, \mathrm{m \, s^{-1}}$). The width of the turbulent plume is estimated to be 9 m (see calculations in Sect. 2.1 below), thus we can estimate that each sperm whale has the potential to influence mixing in a body of water of $2.1 \times 10^4 \, \mathrm{m^2}$ per dive (9 m × 2310 m). Given that dive cycles occur on average once every 67 min, the whale path equates to $1.6 \times 10^8 \, \mathrm{m^2 \, yr^{-1}}$ ($2.1 \times 10^4 \, \mathrm{m^2} \times 21.5$ dives per day × 356 days per year). The 80 sperm

whales that inhabit the waters of Hawaii thus have the potential to influence mixing in an area of 1.3×10^{10} m^2 ($80 \times 1.6 \times 10^8$ m^2). This area (the whale path) is thus the area of water over which a sperm whale travels and we now estimate the extent to which whales influence mixing and nitrogen transport within this area of water.

3.1 Diapycnal diffusivity

The increase in diapycnal diffusivity (K_{sw}) along the whale path caused by whales ascending or descending through a nutricline can be estimated using Eq. (1)

$$K_{sw} = S \times T_d \times N \times V \qquad (\text{m}^2\,\text{s}^{-1}) \tag{1}$$

where S is the average ascent/descent speed of a diving sperm whale (m s^{-1}), T_d is the proportion of time a whale spends diving, N is the density of whales (m^{-2}) along the whale path, and V is the volume of the turbulent wake behind a swimming sperm whale (m^3). The average swimming speed (S) of a diving/ascending sperm whale is 1.54 m s^{-1} (Miller et al., 2004). To calculate the proportion of time spent diving and ascending (T_d), we consider that sperm whales spend 75 % of their lives foraging and, when foraging, typically engage in 50 min dive cycles which include 15 min spent ascending and descending (Whitehead, 2003). T_d is thus estimated by $0.75 \times (15/50) = 0.23$. The 80 sperm whales in Hawaii influence an area of water of 1.6×10^8 m^2 yr^{-1} (see Sect. 2 above) and thus whale density is 6×10^{-9} m^{-2} along the whale path.

The lack of flow visualisation experiments on sperm whales make it challenging to accurately determine the volume of the turbulent wake (V) behind a swimming whale, however, it can be approximated using Eq. (2)

$$V = (\pi \times 0.5W \times 0.5F) \times L \qquad (\text{m}^3) \tag{2}$$

where W is the width of the turbulent wake (m), F is the fluke spread (m) and L is the length of the turbulent plume behind a swimming whale (m). Flow visualisation experiments have shown that the width of the turbulent wake is at least twice the maximum

excursion (peak to peak amplitude) of the tail flukes (Anderson et al., 1998; Taylor et al., 2003; Bandyopadhyay and Donnelly, 1998). The maximum excursion of the tail flukes can be determined by multiplying the body length by the Strouhal number (Rohr and Fish, 2004). We assume a Strouhal number for sperm whales of 0.3 (Rohr and Fish, 2004) and a body length of 15 m (Gosho et al., 1984), giving a maximum excursion of 4.5 m and a wake width (W) of 9 m. The spread of the flukes (F) is estimated at 1/5 of the body length (Nishiwaki, 1972), equating to approximately 3 m in adult sperm whales. The length of the turbulent wake (L) behind a spheroid body is typically estimated at 10 times the body diameter (Chernykh, 2006). Bose et al. (1990) lists the sperm whales maximum girth as 7.8 m, equating to a diameter of approximately 2.5 m. Thus, the volume of the turbulent plume behind a swimming sperm whale (V) is thus estimated by $V = \pi \times (4.5\,\text{m} \times 1.5\,\text{m}) \times 25 = 530\,\text{m}^3$. These calculations can be used to provide an estimate of the diapycnal diffusivity resulting from the biomixing of sperm whales (K_{sw}).

3.2 Nitrogen transport

In this section we use nitrogen profiles measured in the Hawaiian ocean (Karl et al., 2001) to estimate the nitrogen transported into the photic zone (N_f) as a result of the diapycnal diffusivity resulting from sperm whale biomixing (K_{sw}). Nitrogen flux across the nutricline resulting from biomixing by sperm whales (N_f) can be estimated by Eq. (3)

$$N_f = K_{sw} \times G \qquad (\text{kg nitrogen year}^{-1}) \tag{3}$$

where G is the nitrogen gradient ($\text{kg N m}^{-3}\,\text{m}^{-1}$) over the pycnocline. We consider the nutricline at Station ALOHA (22°45′ N 158° W) and average publicly available data collected during six Hawaiian Ocean Time-Series research cruises throughout 2008 (Karl et al., 2001). We are interested here in nitrogen transport into the euphotic zone and so consider the change in nitrogen levels across the 0.1 % light level, which occurs at

approximately 125 m depth (Buesseler et al., 2008). Sperm whales pass through this depth as they descend 300 m to 800 m on foraging dives (Whitehead, 2003). We examine recorded nitrogen concentrations measured immediately above the 125 m depth (measurements were taken at depths ranging from 60 m to 121 m) and immediately below the 125 m depth (ranging from 125 m to 161 m) (Karl et al., 2001). After calculating the change over the 0.1 % light level for each of the six cruises (Table 1), we then averaged these to obtain a gradient of 0.015 µmol nitrogen kg^{-1} m^{-1} which is equivalent to a gradient of $G = 2.2 \times 10^{-7}$ kg nitrogen m^{-3} m^{-1}.

3.3 Carbon fixation

The nitrogen flux into the euphotic zone can be used to estimate the amount of primary productivity that would be stimulated as a result of biomixing by sperm whales. The Redfield ratio is used to conservatively (Sambrotto et al., 1993) estimate the amount of carbon fixed in response to the nitrogen mixed into the euphotic zone by swimming sperm whales. The Redfield ratio describes the stoichiometric ratio of carbon to nitrogen in phytoplankton cells as being 106 : 16 (Redfield, 1934).

4 Results and discussion

4.1 Sperm whale mixing, nitrogen transport and primary production

The diapycnal diffusivity caused by each sperm whale moving through the base of the euphotic zone is $K_{sw} = 10^{-6}$ m^2 s^{-1}. The flux of nitrogen transported into the euphotic zone as a result of this diapycnal diffusivity is $N_f = 1.3 \times 10^3$ kg of nitrogen per year per sperm whale which would in turn stimulate 7×10^3 kg of primary production (carbon) per year. The overall contribution of 80 sperm whales to the nitrogen budget of the Hawaiian euphotic zone along the whale path is 10^5 kg nitrogen yr^{-1} which would stimulate production of 6×10^5 kg carbon yr^{-1}.

The nitrogen flux resulting from sperm whales swimming through the pycnocline is modest compared to the dominant modes of nitrogen flux into the Hawaiian photic zone (Fig. 1). Within the 10^{10} m^2 whale path, sperm whales mix 10^5 kg nitrogen yr^{-1} into the photic zone. In contrast, diatom (*Rhizosolenia*) mats migrate between surface waters and the nitrate pools of the deep ocean and transport 3×10^6 kg nitrogen yr^{-1} into the euphotic zone as they do so (Villareal et al., 1993). Nitrogen fixation along the whale path results in an increase of 8×10^6 kg nitrogen available to the euphotic zone per year. Event mixing is the largest contributor of nitrogen along the whale path and results in transport of 2×10^7 kg nitrogen transported into the euphotic zone per year.

4.2 Ecosystem effects of nitrogen transport by sperm whales

While the overall amount of nitrogen transported by sperm whales is moderate, sperm whales spend 75 % of their time engaged in foraging (Whitehead, 2003) and spend only 7 % of each day sleeping (Miller et al., 2008) so their nutrient contribution to the photic zone occurs throughout the day and night on an approximately hourly basis per whale. This is in contrast to the other dominant modes of nitrogen transport which occur only during daylight hours for nitrogen fixation and nitrogen transport by *Rhizosolenia* mats, or on average once per month for event mixing. Thus while nitrogen inputs from sperm whales occur continuously, the nitrogen inputs from nitrogen fixation and migrating diatom mats are absent for approximately 50 % of the time, while nutrient inputs from event mixing are absent for 95 % of the time (Fig. 2).

Spatiotemporal consistency of nutrient supply to the photic zone can be as important in determining the productivity of high trophic level fish stocks as the overall magnitude of primary production (Kioboe, 1993). Phytoplankton have little ability to store nutrients (McCarthy and Goldman, 1979) and so the consistent, albeit low, levels of nutrient inputs that occur as a result of sperm whale-induced diapycnal mixing may allow phytoplankton to survive periods when other sources of nutrients are absent. When background levels of nutrients are undetectable, phytoplankton are particularly proficient in exploiting spikes of nutrients (McCarthy and Goldman, 1979) by increasing

their nitrogen affinity to quickly utilise a nutrient pulse at rates greater than the steady growth rate (Raimbault and Gentihomme, 1990). The low levels of nitrogen introduced by swimming sperm whales are thus likely to be assimilated quickly and efficiently into phytoplankton cells where they can contribute to ecosystem productivity.

5   Sperm whales likely mix nutrients directly into the deep chlorophyll maximum and the high numerical density of phytoplankton cells in the deep chlorophyll maximum may mean that nutrients are quickly taken up by phytoplankton and that subsequently there is rapid stimulation of primary production. The deep chlorophyll maximum is located immediately above the pycnocline in the Hawaiian ocean (Huisman et al., 2006).

10 Mixing by whales is likely to be effective at supplying the deep chlorophyll maximum with nutrients directly, in contrast to nitrogen fixation which occurs higher in the water column, and event mixing which likely disrupts the deep chlorophyll maximum. Whales thus deliver nutrients to an area rich in phytoplankton cells which can quickly exploit the nutrient pulse (McCarthy and Goldman, 1979).

15 The reduction of sperm whale populations as a result of historical exploitation may have reduced the amount of new nitrogen entering the euphotic zone of the Hawaiian Ocean by reducing whale-induced diapycnal mixing. Worldwide, sperm whale populations have been reduced to approximately 32 % of their historical abundances by commercial whaling (Whitehead, 2002). Assuming this is true for the Hawaiian area, histor-

20 ical sperm whale populations in Hawaii would have once numbered approximately 250. The larger sperm whale populations of the past would have increased diapycnal diffusivity and stimulated the flux of 3×10^5 kg nitrogen yr^{-1} into the euphotic zone. Thus, the Hawaiian ocean has essentially lost 2×10^5 kg of new nitrogen per year as a result of commercial whaling and this has likely decreased primary production in the region

25 by 10^6 kg carbon per year.

Here we have examined the influence of biomixing by a low density population of sperm whales in Hawaii and find that the resulting nitrogen flux is modest compared to the dominant modes of nitrogen flux in the area. However, the methodology introduced here can be easily adapted to determine the contribution of other marine mammals to

diapycnal mixing. Densities of whales in areas such as foraging grounds can be four orders of magnitude greater than sperm whale densities considered here (Nowacek et al., 2011) and this would dramatically increase the amount of diapycnal mixing and the resultant flux of nutrients into the euphotic zone. Sperm whales mix nutrients into the deep chlorophyll maximum throughout the day and night and the consistency of this nutrient input may increase the importance of these nutrients to primary producers above that indicated by examining the magnitude of nitrogen inputs alone. This finding adds to a growing body of knowledge regarding the top-down influence of marine mammals on the nutrient budgets of marine and coastal ecosystems. Whales influence the flux of nutrients in the marine ecosystem by excretion and defecation of nutrients (Smetacek, 2008; Nicol et al., 2010; Roman and McCarthy, 2010; Lavery et al., 2010, 2012a and b), the sinking of their carcass after death (Smith, 1985) and likely via tilling of the ocean floor during foraging (Hans Nelson and Johnson, 1987). Here we added biomixing to these mechanisms and show that it is a source of low magnitude but high frequency nitrogen flux to the euphotic zone of the Hawaiian ocean.

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Table 1. Data obtained from the Hawaiian Ocean Time-Series and used to estimate the nitrogen gradient over the 0.1 % light level which represents the base of the euphotic zone in the Hawaiian ocean.

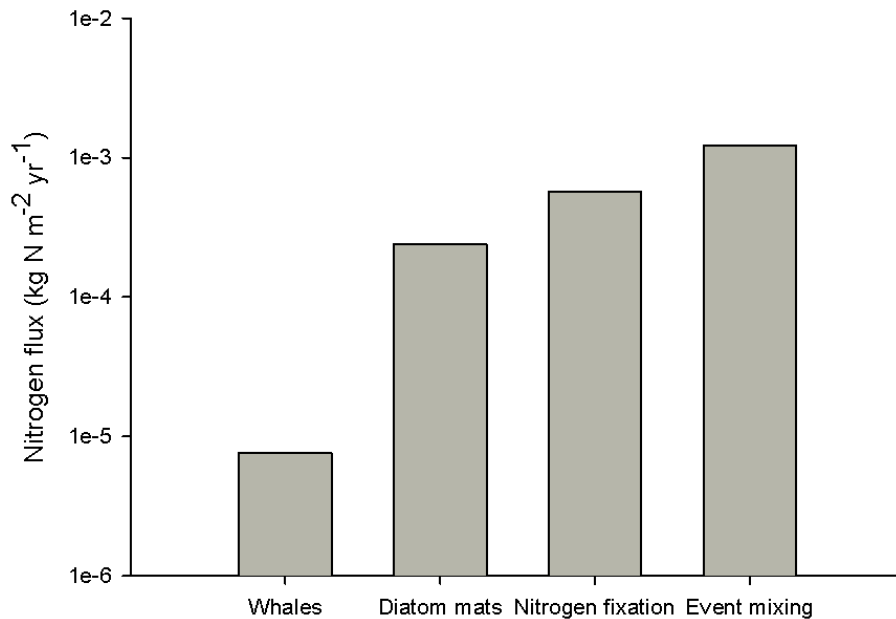| Identification number	Depth (m)	Nitrogen concentration $\mu mol\, N\, kg^{-1}\, m^{-1}$	Gradient $\mu mol\, N\, kg^{-1}\, m^{-1}$
HOT 199	70	0.16	0.02
	125	1.26	
HOT 200	60	0.08	0.11
	126	0.78	
HOT 202	102	0.11	0.011
	135	0.47	
HOT 203	121	0.19	0.007
	161	0.46	
HOT 204	112	0.06	0.0141
	149	0.58	
HOT 205	122	0.45	0.029
	154	1.37	
Average gradient			0.015

Fig. 1. The flux of nitrogen into an area of 10^4 km^2 in the Hawaiian ocean as a result of diapycnal mixing by sperm whales, migration of diatom mats, nitrogen fixation and event mixing.
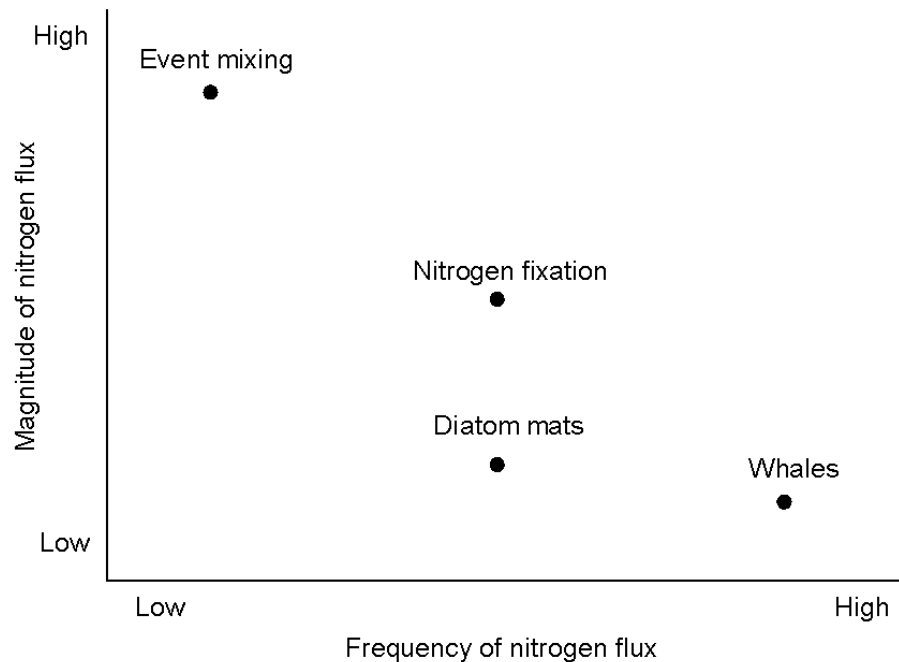
Fig. 2. A comparison of the magnitude and frequency of nitrogen inputs into the photic zone of the Hawaiian ocean as a result of diapycnal mixing by sperm whales, migration of diatom mats, nitrogen fixation and event mixing.