Does the marine biosphere mix the ocean?

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ABSTRACT

Ocean mixing is thought to control the climatically important oceanic overturning circulation. Here we argue the marine biosphere, by a mechanism like the bioturbation occurring in marine sediments, mixes the oceans as effectively as the winds and tides. This statement is derived ultimately from an estimated 62.7 TeraWatts of chemical power provided to the marine environment in net primary production. Various approaches argue something like 1% (.63 TeraWatts) of this power is invested in aphotic ocean mechanical energy, a rate comparable to wind and tidal inputs.

1. Introduction

The deep waters of the world ocean are stratified and, in an insightful paper, Munk and Wunsch (1998; MW98 hereafter) revisited the question of how this stratification is maintained. Ultimately the discussion in MW98 turned to turbulent mechanical energy and the power sources driving that turbulence. The inputs to this energy of physical origin have by now been rather thoroughly examined; we here take a different approach and suggest that a source of biological/chemical origin, i.e. the marine biosphere, is plausibly of comparable importance to the turbulent mechanical energy budget.

a. Background

A well-known feature of the ocean circulation is its meridional overturning cell (MOC hereafter; see Fig. 1), which is, in turn, intimately connected with the deep stratification. There are two thoughts about how the MOC is maintained. One view originally advanced by Toggweiler and Samuels (1998) and Webb and Suginohara (2001) focuses on the surface effects of the wind in the Southern Ocean. The other view, discussed in MW98, and more recently in Wunsch and Ferrari (2004), emphasizes the importance of turbulent mixing, in which heat mixed downward warms mid-latitude abyssal waters and drives an upwelling that balances high latitude deep water formation. While both processes are probably in operation, which one is dominant is not yet clear.

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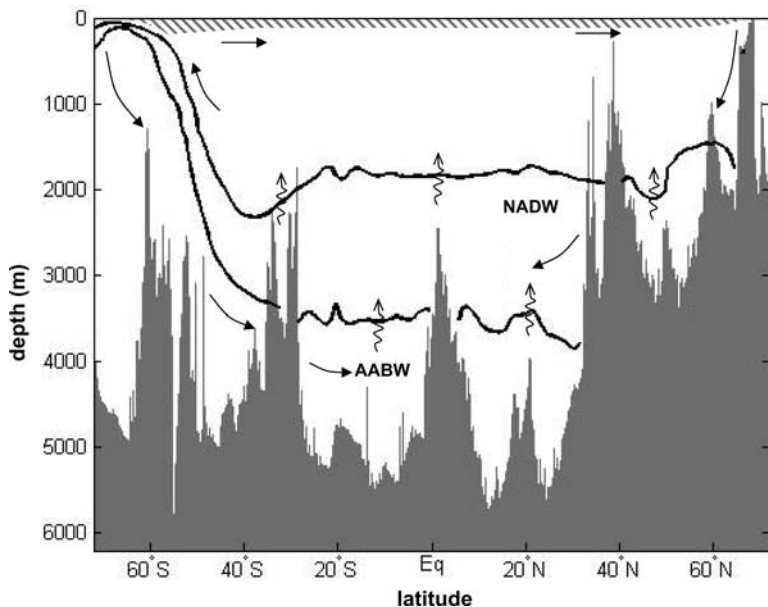
Figure 1. Schematic of the ocean overturning circulation. For certain density ranges, waters are formed in isolated locations, like the far North Atlantic, and upwell at lower latitudes. This component of the overturning circulation requires energy from an external source.

The mixing scenario in MW98, framing the discussion here, most likely determines the deeper stratification, and thus a component of the MOC. This has climatic implications through climate-MOC connections and in part motivates the present work. Crudely speaking, climate is a by-product of a global transport of excess heat from the equator to the poles. While their ratio is debated, the atmosphere and ocean are comparable contributors to this transport (Trenberth and Caron (2001) argue that the atmosphere is the primary contributor and the ocean secondary) and, in the ocean, the MOC is important for heat flux. MOC variability then potentially connects to climate variability, possibly imprinting time scales from years to millennia on the system and synchronizing past glaciations (Broecker and Denton, 1989).

It is also clear that ocean diapycnal mixing, in its vertical transport of buoyancy, must consume energy. MW98 estimate the mixing power requirement at about 2 Terawatts (1 TW = 10^{12} W). Although this number is likely uncertain to a factor of two, St. Laurent and Simmons (2006) use an independent technique and find a comparable, if modestly higher, bulk dissipation ($\sim$2.4 TW). To obtain the total energy flux through the system, these numbers must be augmented by an additional 20% (reflecting an assumed mixing efficiency of $\Gamma = 0.2$) to account for the increase in potential energy associated with the mixing, yielding a total power requirement of 2.9 TW. Again, this number contains large error bars. MOC dependence on mixing differs importantly from classical scaling when energetics constraints are considered (Huang, 1998).

A central issue in the study of mixing then has become the identification of the energy sources providing the needed power. Indeed, this is part of the broader, open question of the ocean energy budget, the clarification of which is of obvious scientific value. Heating and cooling have traditionally been thought to provide the sources of energy for the MOC but theory suggests otherwise (Sandström, 1916; Paparella and Young, 2002). MW98 instead argue winds and tides provide about 1 TW each to mixing, resulting in a total power that is a substantial fraction, and perhaps all, of the energy apparently needed to mix the deep ocean. With one possible exception, other physical sources, like geothermal heating, appear to be weak (Huang, 1999; Wunsch and Ferrari, 2004). The exception is the mesoscale, whose energy is ultimately provided by the large-scale winds. Wunsch (1998) estimates energy moves through the mesoscale at a rate of about 1 TW. How this energy gets out of the mesoscale is, however, unclear and it is unknown if this is a significant contributor to the turbulent ocean mechanical energy budget.

Although sources yielding net power close to the apparent requirement have been identified, there are several reasons to believe the budget is not yet balanced. For example, it is not clear if all the energy lost to the ocean from the winds and tides is spent on mixing. Baroclinic tides are generated with vertical scales of kilometers, whereas dissipation in the open ocean occurs on the Kolmogorov scale $L_K = (\nu^3/\varepsilon)^{1/4}$, where ν is the molecular viscosity of sea water (10^{-6} m^2/s) and ε is the dissipation rate. For oceanic parameters, $L_K \sim 5$ mm. Stratification influences the turbulence down to the Ozmidov scale, $L_o = (\varepsilon/N^3)^{1/2} = 0.3$ m. Energy in the baroclinic tides can reach small scales through the forward cascade of the internal wave field. This, however, requires time and along the way significant amounts of energy may well dissipate against topography or boundaries thereby reducing the tidal mixing contribution. Wind energy enters at the ocean surface and may also experience loss while propagating to depth. Winds and tides are undoubtedly important to ocean mechanical energy, but there is reason to suspect important energy sources remain undiscovered. If sources are found that also naturally operate at mid-depths and inject energy at small mixing scales, so much the better for their relevance to mixing.

Here, we argue the biosphere is such a source. Specifically, by kinetic expenditures (i.e. locomotion, reproduction) in the mesopelagic ocean, we suggest marine life contributes to the mechanical energy needed to mix the ocean at a rate comparable to the winds and tides. Such biological processes were known to Munk (1966), but his focus was the ocean beneath 1000 m and he concluded they were probably negligible. Here, for definiteness, we take the term 'deep ocean' to be synonymous with the aphotic ('unlit') ocean, i.e. any place deeper than $\sim$200 m. While this spans a portion of the water column not traditionally thought of as the 'abyssal' ocean, it is a usage consistent with many statements in Wunsch and Ferrari (2004), while clearly including shallower reaches of the ocean than Munk (1966) considered. As will be discussed shortly, the focus on the aphotic ocean is also convenient when interpreting biological activities.

2. Ocean mixing by the marine biosphere: An anecdote

The net biosphere energy input is analyzed below; here we illustrate our thinking by a dramatic example. There are currently 360,000 sperm whales (*Physeter macrocephalus*) in the world ocean (Whitehead, 2002) with an average mass of 40 T ($1T = 10^3$ kg) per whale. They are aggressive hunters, hunting at depths of about 1 km and it is estimated that they spend 80% of their lives beneath 500 m (Whitehead, 2004). We assume when averaged over all sperm whale swimming behaviors, they invest energy at a rate ~5 kW/whale ($1 kW = 10^3$ W) against locomotion in the aphotic ocean. There are many bits of evidence arguing this number is not an overestimate. (1) For example, from observations of marine mammals cost of transport, *COT*, is

$$COT = 0.2 \times 0.6 \times 7.79 \, M^{(-0.29)} \, (COT \text{ in J/kg/m, } M \text{ in kg})$$

where the first two factors correct for surface wave drag and internal maintenance (Williams, 1999). For a 40 T sperm whale swimming at 2 m/s, $COT = 3.4$ kW. (2) Sperm whale basal metabolic rate (*BMR*) as predicted by the Kleiber curve is $BMR = 2 \times 70 \, M^{3/4} = 20$ kW (*BMR* in kcal/day, M = mass in kg, Kleiber, 1932), where the first factor corrects for a possible marine mammal bias. Swimming costs are at least 20–25% of *BMR*, yielding 4–5 kW as a conservative estimate. (3) Direct observations of sperm whale ascents and descents yield drag losses of ~1 kW (Miller *et al.,* 2004). (4) Fish (1998) measured thrust from a variety of hunting whales (but not sperm whales), finding at full throttle they expended 4.4 W/kg against drag. For a 40 T sperm whale, this implies 176 kW. The mechanical energy generation rate from a sperm whale ultimately reflects a weighted average over all injections, arguably ranging from 1 kW to 176 kW. The weighting is no doubt heavily biased toward the lower values, as full throttle swimming is confined to special activities, like the final chase during predation. Considering these numbers, 5 kW seems a reasonable estimate of an average sperm whale swimming energy flux to the environment.

Hence, sperm whales alone contribute $0.8 \times 360000 \times 5kW = 1.44$ GW (1 GW = 10^9 W) to deep ocean energy. Sperm whales exhibit hunting and swimming behaviors similar to approximately 60 species of smaller, but more numerous, toothed whales. All dive to aphotic depths; several dive to sperm whale depths (1–2 km). Assuming toothed cetaceans average 20% of the sperm whale contribution (allowing for shallower diving and less time at depth), this small fraction of the marine biomass adds 17 GW, or ~(0.5–1%), of the 2–3 TW global mixing requirement, to the aphotic mechanical energy budget. In comparison, Hawaii by scattering of the barotropic tide into baroclinic modes contributes 18 GW (Egbert and Ray, 2000).

Although anecdotal in nature and carrying large, uncertain error bars, the above both illustrates our thinking and emphasizes that the biosphere input to mechanical energy is quite likely of significant magnitude. But the point of this paper is not that 'Whales mix the ocean.' Instead, we argue important contributions to the mechanical energy budget are

made across the biosphere and all the way down to the zooplankton. The participation of the zooplankton might appear surprising since they are typically thought of as relatively small ($\sim 10^{-2}$ m) and thus their movements might well inject kinetic energy at such small scales that they do not effectively mix the tracer field. We include them here because many of the aggressive and active zooplankton are larger than 10^{-2} m and, as argued earlier, the Ozmidov scale down to which important tracer mixing occurs, at 0.3 m, is surprisingly small.

To arrive at a net estimate of the biosphere contribution to mechanical energy, one could in principle continue the approach used on sperm whales species by species and ultimately sum the results. But, it is neither practical nor particularly convincing to do so. Rather, we describe below an equivalent global approach that captures all such inputs while simultaneously compressing the problem to a small set of (admittedly poorly known) numbers. We also emphasize at the outset the uncertain nature of the estimates we are to make. In fact, it is arguable whether or not uncertainties can be reliably assessed; they depend upon such things as bulk locomotion efficiencies, obtained by averaging over all body types in the marine environment, from highly efficient sharks to presumably inefficient jellyfish. This issue has been raised by a reviewer, who subsequently questioned if anything in this paper could be believed. We agree with this concern but nonetheless find the numbers appearing below to be sufficiently intriguing that we believe they deserve consideration in the literature. We have also attempted consistently to adopt conservative values when making estimates and to obtain independent estimates of biopower when possible.

3. Global analysis: An energy equation in bio-space

Consider any member 'n' of any marine species 'i'. The energy content, E_i^n, of this organism obeys

$$[E_i^n]_t = \sum_{j,m} \alpha_{i,n,j,m} E_j^m - TMR_i^n - L_i^n + P_i^n + \sum_{j,m} g_{i,n,j,m} L_j^m - B_i^n \qquad (1)$$

where the subscript 't' denotes a time derivative. The first right-hand-side quantity denotes predation, where fraction $\alpha_{i,n,j,m}$ (per unit time) of member 'm' of species 'j' is consumed by member 'n' of species 'i', B_i^n denotes birth loss, TMR_i^n total metabolic requirement, L_i^n chemical loss (egestion and excretion), P_i^n photosynthesis and $g_{i,n,j,m}$ consumption by this organism of the waste products of others (also called coprophagy). Of course, for many species, some of these terms will vanish (e.g. sharks don't photosynthesize).

Summing on 'n' yields an energy budget for an entire species,

$$[E_i]_t = \sum_{n,j,m} \alpha_{i,n,j,m} E_j^m - TMR_i - L_i + P_i + \sum_{n,j,m} g_{i,n,j,m} L_j^m - Lim_{\delta t \to 0} \sum_1^{M_i \delta t} \frac{E_i^{n\partial}}{\delta t}. \qquad (2)$$

The last term represents mortality energy loss at rate M_i from 'i' due to predation and senescence. Births disappear as they only redistribute energy within species 'i'.

The energy budget for the entire marine biosphere is obtained by summing on 'i'

$$E_t = P - TMR - L - MT \tag{3}$$

where L represents burial losses from the biosphere to the lithosphere and MT the energy flux from the marine biosphere to the terrestrial biosphere due to grazing. Chemical grazing and predation vanish from (3) as they create no energy, and serve only to redistribute it within the marine biosphere.

Assuming the budget in (3) is static, the lone energy source P (photosynthesis) is balanced by TMR losses, burial and loss to the terrestrial biosphere. Major contributors to MT include fish consumption by marine birds and human fishing activities. Considering the latter, global annual ocean catch is currently about 85 Mtons (see *http://www.fao.org/fi/ statist* of the United Nations Food and Agricultural Organization). Assuming an average energy density of 8 MJ/kg, this implies a 'terrestrial grazing flux' of $MT = 22\ GW$.

To the extent MT is negligible (as will be argued shortly), the implication of (3) is that the total metabolic activity capable of being expended by all organisms in the marine system is capped by the rate at which the photosynthesizers sequester energy.

a. Net primary production as a cap on metabolic activity

While the idea behind (3) is useful, by definition all photosynthesis occurs in the euphotic ('lit') ocean by phytoplankton that are largely incapable of self propulsion. In contrast, our interests are ultimately in the turbulent mechanical energy of the aphotic ocean, implying a more relevant limit to power for current purposes entails the energy left over by the photosynthesizers after they have been sated. A step toward correcting for this is achieved by summing (2) only over the phytoplankton and zooplankton (which will frequently be referred to here as trophic levels 1 and 2). Assuming again a static budget, the result is

$$P - \sigma_p TMR_i = \sigma_z \sum_m \delta_{j,m} L_j^m + Lim_{\delta t \to 0}(\sigma_p + \sigma_z) \sum_m^{M'_j \delta t} \frac{\Delta_{j,m} E_j^m}{\delta t} + \sigma_z TMR_i$$

$$+ Lim_{\delta t \to 0}(\sigma_p + \sigma_z) \sum_m^{M''_j \delta t} \frac{E_j^m}{\delta t} - \sigma_z \sum_n \sigma_{\neq} \sum_m g_{i,n,j,m} L_j^m \tag{4}$$

where $\sigma_{(p,z,\neq)}$ denote partial sums over phytoplankton, zooplankton and other species, respectively. '$\Delta_{j,m}(\delta_{jm})$' denotes zooplankton feeding inefficiency (also called 'sloppy eating') and $M'_{jm}(M''_{jm})$ denotes mortality due to zooplankton (other species) predation. The left-hand side of (4) literally represents the net energy produced by the phytoplankton, *i.e.* gross energy fixation by the phytoplankton adjusted for what the phytoplankton themselves burn in metabolic activity. The biological community refers to this as net primary production (*NPP*) and usually expresses it in terms of carbon. Here, *NPP* will be interpreted in terms of energy.

The next line includes net senescence and sloppy eating from the phyto and zooplankton; of particular interest to us is the component departing the euphotic ocean, usually called 'the biological pump,' or 'export carbon flux.' Normally, the pump is recognized as a carbon burial mechanism; here we focus on its energetic consequences. After feeding inefficiencies comes zooplankton *TMR* and net energy flux to higher trophic levels.

How much energy is contained in *NPP*? This may be estimated from satellite based ocean color observations that, in turn, are related through models to *NPP*. Our calculation of the oceanic *NPP* distribution, based on the Moderate Resolution Imaging Spectro-Radiometer (MODIS) color data fed through the semi-analytical model of Behrenfeld and Falkowski (1997) appears in Figure 2a (see also Behrenfeld *et al.,* 2001). Variations from less productive mid-latitudes to highly productive equatorial and subpolar zones are observed. We have averaged these values over locations where the ocean depth exceeds 500 m, according to the ETOPO5 data set, yielding an average (integrated) *NPP* of 0.16 kgC/yr/m^2 (49 GtC/yr, 1 Gt $= 10^{12}$ kg). Our estimate is in agreement with other estimates of global *NPP*, both *in-situ* and remote.

NPP carbon is a mix of proteins, carbohydrate and lipids occurring in phytoplankton in roughly equal amounts. The carbohydrates are essentially the end-product of photosynthesis, a chemical cycle which has been studied extensively and is known to sequester energy at the rate of approximately 115 kCal/mole C. Carbohydrates have the lowest energy density while lipids and proteins are richer per unit mass, but involve more moles of carbon. A reasonable estimate of the energy contained in *NPP* may then be obtained by using the photosynthetic energy fixation rate, which yields

$$NPP = 49 \text{ GtC/yr} \times 115 \text{ kCal/mole C} = 62.7 \text{ TW}$$

or 205 mW/m^2 (1 mW $= 10^{-3}$ W) when normalized by the deep ocean area (3.1 $\times$ 10^{14} m^2). For comparison, estimates of wind input to the ocean vary from 7-36 TW (Lueck and Reid, 1984) to 60–64 TW (Wang and Huang, 2004a,b). Tidal forcing adds ~1 TW to the deep ocean. Of course, conversion mechanisms of these sources to mechanical energy capable of stirring tracers will differ greatly, so a simple comparison of net inputs is incomplete in itself. On the other hand, the biosphere clearly emerges as an intriguing potential mixing source based on *NPP* power alone. Note also, the terrestrial grazing flux of 22 GW is comparatively small, and will be neglected from now on.

b. How much bio-power does the aphotic ocean receive?

The photosynthetic power in *NPP* is stored as chemical energy and enters the oceans in the upper 200 meters; we now estimate the fraction of *NPP* contributed to the aphotic mechanical energy budget. To this end, three arguments are used employing three independent approaches and observations. The first two evaluate specific pathways and the last considers all inputs.

i. Aphotic ocean mechanical stirring by nekton. Regarding feeding inefficiency, it is convenient to consider the euphotic and aphotic oceans separately. The detrital exchange
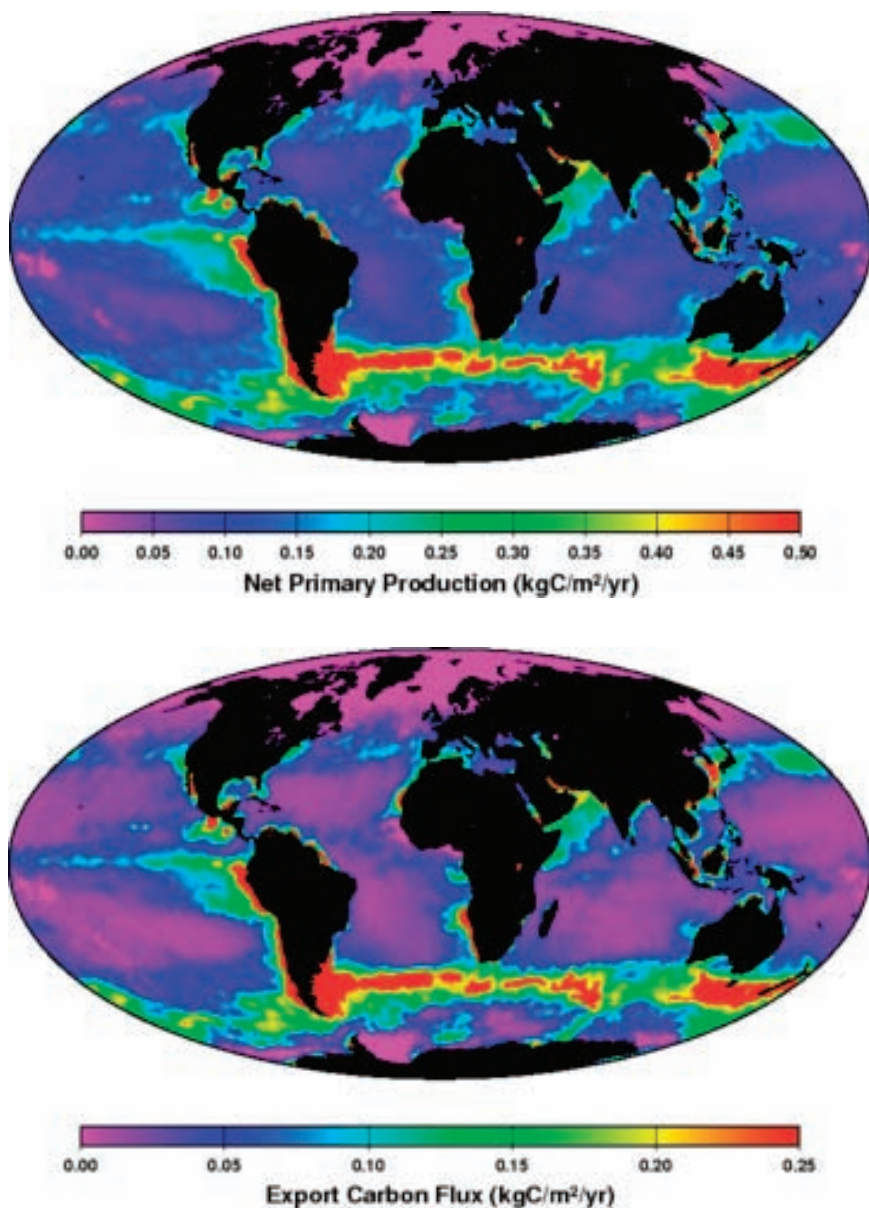
Figure 2. (upper) Ocean net primary production derived from the MODIS (Moderate Resolution Imaging SpectroRadiometer) satellite using the semi-analytic model of Behrenfeld and Falkowski (1997). The average net primary production in the deep-ocean is 0.16 kgC/m^2/yr. (lower) 'Export carbon' as calculated from (a) using Eppley and Peterson (1979). According to this formula, roughly 16 GtCyr^{-1} (0.064 kgC/m^2/yr) are exported from the euphotic zone to the deep ocean. Other relations yield lower net export flux (we use 11 GtC/yr), but the spatial patterns remain as shown.

between them is known as the export carbon flux. Many past studies have attempted to relate export carbon to *NPP*, and hence to satellite observations of ocean color (Eppley and Peterson, 1979; Antoine and Morel, 1996; Falkowski *et al.,* 1998; Laws *et al.,* 2000). From such studies and our own evaluation of the MODIS data (see Fig. 2b), a net export carbon flux of 11 GtC/yr, as found from the ET model in Laws *et al.* (2000), seems reasonable. For comparison, the ETP model in Laws *et al.* (2000) yields 9 GtC/yr and the EP model 16.9 GtC/yr. Much of the pump is plant material, and hence represents an energy flux that may be estimated using the above photosynthetic energy fixation rate. Thus, the carbon pump energy flux is approximately 45 mW/m^2 (14 TW).

The carbon pump is composed jointly of dissolved (*DOC*) and particulate organic carbon (*POC*) with the dominant contribution (~90%) in the latter category. A major distinction between *POC* and *DOC* is *POC* falls through the water column at finite speeds. However, it is also observed in sediment trap data that *POC* density decreases with depth; most (90%) of the carbon is gone by 1500 m (70% by 500 m) and little (<4%) escapes to the lithosphere (Iverson *et al.,* 2000). Allowing for *DOC* and burial, the sediment trap data argues the pump constitutes a 12 TW energy flux divergence in the aphotic ocean.

The size of the particulate matter determines its fall rate, centered on 100 m/day. Hence, in 20 days the particulate material disappears and 12 TW are shunted to the environment. Ultimately the flux is 'remineralized' by bacteria; but we now argue the bulk of the energy goes elsewhere. The basis of this argument is that bacteria are relatively inefficient at *POC* consumption, obtaining the bulk of their diet from *DOC* and general coprophagy of the waste from higher trophic levels.

The immediate fates of the *POC* flux are direct bacterial uptake (*BD*), consumption by zooplankton (*ZG*) and consumption by (primarily small) fish (*HTG*), i.e. trophic levels 3 through 5

$$POC = BD + ZG + HTG. \tag{5}$$

Typical trophic level theory recognizes *TMR* as the dominant energy sink of a trophic level, with grazing to higher trophic levels and chemical loss being far smaller. To exploit this, (5) is rewritten as

$$POC = BD + ZL + ZTMR + ZHTG + HTG$$

where *ZL* denotes zooplankton chemical loss, *ZTMR* zooplankton metabolic activity and *ZHTG* grazing by higher trophic levels of zooplankton. Lefevre *et al.* (1996) and Sheridan *et al.* (2002) find *POC* constitutes less than 20% of the total bacterial energy intake. Using standard estimates (*TMR* ~70% of total energy flux, grazing ~ 10% of total energy flux, Russell-Hunter; 1979), zooplankton chemical loss, *ZL*, is ~20% of total zooplankton energy flux. Assuming that zooplankton chemical loss (*ZL*) then makes up the balance of the bacterial energetic requirement, 0.8 *BD* = 0.2 *ZG*. If we further neglect the direct

feeding on POC by trophic levels 3 and higher, $HTG = 0$, (an assumption which for our purposes is conservative as explained below)

$$POC = 12\text{TW} = 0.25ZG + 0.7ZG + 0.1ZG = 1.05ZG \qquad (6)$$

implying higher trophic level intermediaries (here 2nd trophic level only) process $ZG \approx$ 11 TW of the export carbon in the aphotic ocean.

If we now assume that these zooplankton are consumed in the aphotic ocean by higher trophic levels, the above grazing flux efficiency of 10% implies ~1.1 TW powers the deep ocean trophic levels 3 through 5. Here it is seen why our neglect of the direct consumption of the export carbon energy flux by the higher trophic levels is conservative; any energy so grazed adds to the higher trophic level energy at 100% efficiency, rather than having 90% of that energy stripped away in the form of zooplankton TMR and chemical loss.

The fate of this power is higher trophic level TMR and chemical loss, of which we assume the latter is negligible. A principle kinetic activity of these organisms is swimming, an activity that has been the subject of much biometric study. Total metabolic rates of active marine animals (including marine mammals) are typically 2 to 3 times basal rates (Lowe, 2001; Williams, 1999), implying that 60–70% of TMR is associated with swimming. Routinely, between 10% and 25% of the metabolic energy released in muscles by fish (i.e. (6–18)% of TMR) is used to overcome drag (Alexander, 1967; Blake, 1983). The efficiency of swimming fish (defined as work against drag divided by total mechanical work introduced to the environment) runs between 0.4 and 0.8 (Blake, 1983; Huntley and Zhou, 2004). Hence, the range of TMR invested as mechanical energy in the environment is between $6\% \times 1.25 = 7.5\%$ and $18\% \times 2.5 = 45\%$.

The true mechanical energy investment over the higher trophic levels from swimming is a mass weighted average over those levels; and thus should be weighted toward the smaller, and thus less efficient locomotors that make up the greatest biomass fraction of trophic levels 3–5. We take 15% as an estimate of that average. In comparison, Munk (1966) used 20%. From our number, we expect 1.1 TW $\times$ 0.15 ~165 GW to aphotic ocean mechanical energy by deep ocean higher trophic level swimming powered by export carbon. Our earlier anecdotal sperm whale example contributes to this part of the budget.

ii. Diel vertical migration by zooplankton. Consider next zooplankton TMR. As emphasized by Wiebe *et al.* (1979), many zooplankton species exhibit dramatic diel migrations, moving from the surface at night, to depths of 500 m and beyond in the day. The apparent motivation behind this migration is the evasion of predation. Diel migrations have been recognized as a global phenomenon for many years and include the plentiful and globally distributed euphausiids, copepods, and salps. The biomass fraction of zooplankton exhibiting such migrations is uncertain. Wiebe *et al.* (1979) found 90% of slope water zooplankton biomass moved beneath 500 m on a daily basis, although this most likely represents an upper bound rather than a typical migration. Ianson *et al.* (2004) argue from other measurements that 15% of the zooplankton biomass migrates. The assumptions employed

in this estimate are conservative, making it likely not to be an overestimate. In what follows, we use 10% as representative of the zooplankton biomass fraction that are migratory.

The dominant energetic sink of any one trophic level is bulk metabolic activity, here represented for zooplankton by $\sigma_z TMR$ in (4). Typically 70% of the energy of any trophic level is expressed as TMR, which given our 63 TW starting point implies 44 TW. Consider the implications of a 40 TW TMR zooplankton loss. With 10% of the zooplankton spending half a day in the aphotic zone, losing 20% of TMR to locomotion, 400 GW are added to the aphotic zone mechanical energy budget. It will be recognized that this contribution is sensitive to the assumed 20% efficiency of locomotion, again the same value Munk (1966) used to characterize zooplankton. It is also a number comparable to, if slightly higher, than that used for higher trophic level swimmers, but zooplankton are different in swimming behaviors from nekton, so it is not clear the same value should apply.

Therefore, we have also considered zooplankton mechanical energy input by modelling them as bluff bodies. A quick perusal of photographs of many euphausiids, etc. argues convincingly that they are not particularly hydrodynamic or streamlined in design, consistent with the use of bluff bodies. A key parameter in bluff body modeling is the Reynolds number, $Re = UL/\nu$, where ν is the molecular viscosity of water (10^{-6} m^2/s), U is the flow speed and L a representative length scale. Wiebe *et al.* (1979) observed sustained migratory speeds of 0.16 m/s for their zooplankton. With a representative length scale of .01 m, $Re = 1600$. Other zooplankton move more slowly, but can be bigger and all exhibit bursts of speed under special circumstances (such as predation evasion), which are well in excess of their sustained speeds. Accounting for this variability, Re is roughly (200–5000).

In any case, this is a Reynolds number range where wind tunnel experiments show the effective coefficient of drag on a bluff body is ~1 (Batchelor, 1970). Thus, the drag D on the body is given by $D = 0.5\rho A U^2$, where ρ is the density of water (assumed to match that of the zooplankton), U is the zooplankton swimming speed and A is a representative cross sectional area. The quantity A scales with zooplankton volume, V, as V/a, where 'a' is the zooplankton length scale. The product ρV naturally occurring in drag can be equated to the mass of an individual zooplankton, hence $D = dm_i\, U^2/a$, where dm_i is the mass of zooplankton individual i.

Energy loss to the environment due to drag is given by the product DU. For a zooplankton population, averages over the collection must be taken, so the net energy scales as $\langle U^3 \rangle$, where the angle brackets denote an expected value. Note, we neglect mass and length scale variability in considering only velocity fluctuations. Zooplankton are also relatively inefficient swimmers, thus investing mechanical energy in the environment in excess of that needed to overcome drag by a factor of roughly $(eff)^{-1} = 3$ (Huntley and Zhou, 2004).

The expected vertical zooplankton swimming speed, $\langle W \rangle = \langle U \cos\theta \rangle$ where W is the vertical speed of a body moving with speed U and direction θ with respect to vertical, of many zooplankton types has been observed. $\langle W \rangle$ runs from 0.16 m/s for salps (Wiebe *et al.,* 1979) to 0.03 m/s–0.06 m/s for copepods and euphausiids (Wiebe *et al.,* 1992). We have computed the expected swimming speed $\langle U \rangle$ from $\langle W \rangle$ assuming both U and θ are independent Gaussian distributed random variables. Speed variances from 5% to 75% of $\langle U \rangle$ and direction variances from 0° to 90° were explored. Knowing $\langle U \rangle$ permits a straightforward calculation of $\langle DU \rangle_i = dm_i \langle U^3 \rangle / a$, the environmental energy investment of organism '*i*'. Thus, with knowledge of zooplankton biomass, one can obtain a net environmental energy flux.

How much zooplankton biomass is there? Blackburn (1981) provides columnar estimates for open ocean environments ranging from .01 kg/m² to .15 kg/m². If we assume an average zooplankton concentration of 0.1 kg/m², a global zooplankton biomass of 30 Gt is obtained, from which we estimate there are 3 Gt of migrators (.01 kg/m²). An order of magnitude argument supporting the above zooplankton concentrations levels appears in Appendix I.

The computed mechanical power investment as a function of speed variance and direction variance for $\langle W \rangle = .06$ m/s appears in Figure 3. The range is from 50–1800 GW, the latter occurring for speed variances of 0.042 m/s. For this variance, speeds as large as 0.16 m/s occur less than 1% of the time, yet it is known these speeds typify the sustained swimming speeds of the migrating salps. In view of this, mechanical energy fluxes of ~.50 TW do not seem unreasonable.

In much less detail, adopting a zooplankton migration speed of 0.1m/s, the energy flux from the migrating zooplankton, P_z, is

$$P_z = \frac{0.5\, M_2 U^3}{(a)\,(eff)} \approx \frac{1.5 \times 10^{12}\, \text{kg}\ 10^{-3} \text{m}^3/\text{s}^3}{.01\ \text{m}\ 0.3} = .45\text{TW}$$

where M_2 is the migrating zooplankton biomass. The power from this simple estimate is much like the value obtained with more detail above.

iii. Total metabolic energy release. Last we consider an estimate based on an entirely independent set of measurements, i.e. those of oxygen utilization rate (OUR). The philosophy here is that the oxygen sink in the ocean is biological respiration. Water assumed to be saturated in oxygen at the surface, when subducted, then decreases in oxygen to subsaturated values due to any and all types of biological activity.

Jenkins (1982) argues how the age since subducted of a water mass can be estimated from transient tracer information, from which the rate of oxygen consumption (OUR) can be estimated. Jenkins finds column integrated North Atlantic Sargasso Sea and Beta Spiral region aphotic zone OURs of 5.7 μmoleO$_2$(kg yr)$^{-1}$. Rates for the Pacific are comparable, if lower, at 3.2 μmoleO$_2$(kg yr)$^{-1}$ (Sonnerup *et al.,* 1999). Interestingly, the observations
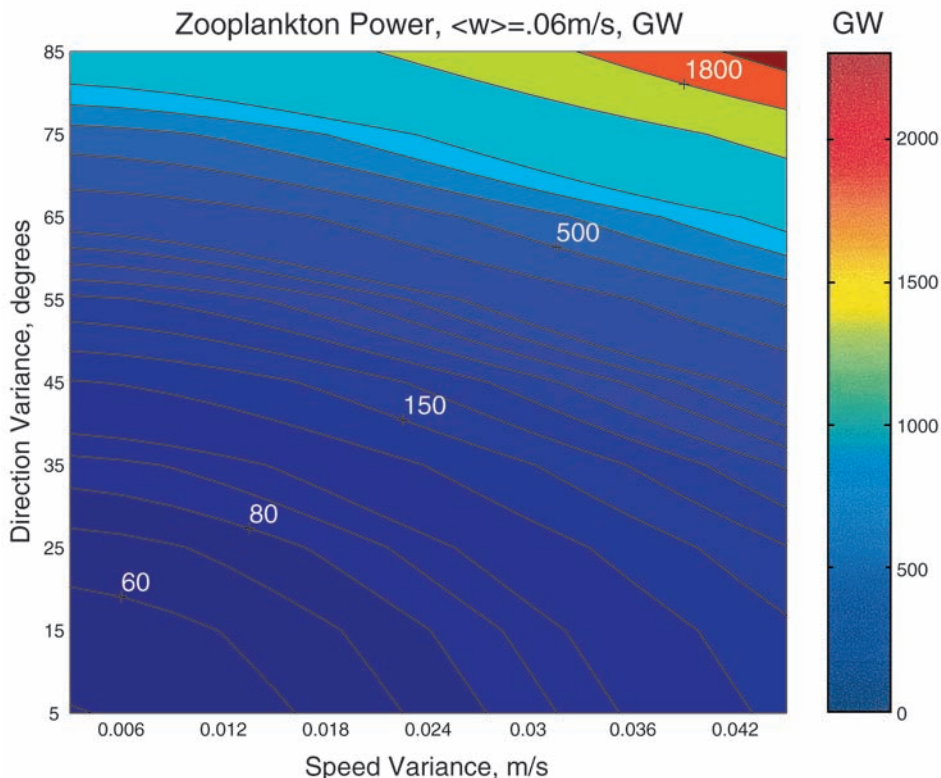
Figure 3. Zooplankton mechanical power versus speed and direction variance. The empirical formula for net zooplankton work against the environment, $P_z = I \int 0.5 \, U^3 / a \, dm$, where U is zooplankton swimming speed, dm is the mass of an individual, a is the zooplankton lengthscale (here taken as 0.01 m), P_z is net power and I is an inefficiency factor (here taken to be 3), is plotted in GW. Zooplankton swimming speed and direction are assumed to be uncorrelated Gaussian random functions with the root mean square variances displayed on the axes. It is assumed that the expected vertical swimming speed is .06 m/s. The observed range is .03 m/s − .16 m/s. The values run in the 100's of GW for reasonable parameters.

behind both estimates come mostly from the relatively inactive interior oceans, as seen by the MODIS satellite, suggesting these values do not overestimate the global OUR.

The chemistry of respiration is, like photosynthesis, well known and releases energy at a rate of approximately 19 kJ/(Liter O_2) (1kJ = 1000 Joules). This value is on the low end of the range, with higher values by roughly 10% possible depending on the quality of the tissue being consumed. The above North Atlantic and North Pacific OUR's correspond to global releases of 25 TW and 15 TW, respectively. Further, these are representative of energy releases in the aphotic ocean, as the depths at which the OUR rates are obtained correspond to depths beyond 200 m. From the above discussion, the average value of 20 TW seems a reasonable estimate of the global aphotic ocean biological energy release.

Note, this number is apparently larger than the energy flux implied by the export carbon flux (12 TW) summed with the migrating zooplankton (2 TW). Of course, uncertainties on all these numbers are large, so it is unclear if the difference is statistically significant. On the other hand, there are several pathways aside from the two we have previously considered, thus suggesting the difference reflects these pathways and is real. For example, the highest biodensity is located in the euphotic zone, and considerable higher trophic level feeding takes place there. A fraction of *TMR* so powered will be expended in the aphotic ocean as the nekton in question swim in the unlit ocean. Similarly, the shallow oceans and continental shelves are amongst the most productive of the oceanic zones. It can be anticipated that there will be a net export of energy off the shelves and into the deep ocean. We have further neglected any direct feeding of the higher trophic levels on the export carbon and we have ignored any mechanical energy flux to the deep ocean caused by permanently resident nonmigrating zooplankton.

Of the 20 TW implied by the OUR observations, some drives bacterial metabolism. Previously we have estimated 2 TW of 14 TW goes to bacteria from export carbon. Of the remaining 6 TW, the fraction going to bacteria can be estimated as that due to the chemical loss of the higher trophic levels, and thus amounts to about 1 TW. It appears then that easily no more than about 33% of the 20 TW can be bacterial, leaving 14 TW to trophic levels 2–5 to be burned as *TMR*. We have presented arguments previously that the mechanical energy fraction in the marine biosphere ranges around 15–20% of *TMR*. To be conservative, assume the fraction is 10%, yielding a net flux to the aphotic ocean of 1.4 TW.

4. Discussion

Using three independent approaches, we have estimated various contributions from the marine biosphere to the aphotic ocean mechanical energy budget. Two of these approaches are of specific pathways, i.e. higher trophic level swimming fed by export carbon (165 GW) and zooplankton migration (400 GW). The third approach estimates the energy released by all respiration in the aphotic ocean (1.4 TW). The latter, being larger than the sum of the former two, while possibly not a real difference, could represent the contributions of pathways other than those considered explicitly here.

Thus we suggest a net biosphere contribution of ~ 1.0 TW (3.2 mW/m^2) to the aphotic ocean mechanical energy budget. A significant fraction of this is provided by zooplankton, but in view of the uncertainties, we suggest that higher trophic levels and zooplankton are roughly equivalent contributors to the mechanical energy input. For comparison, the input to the aphotic mixing from winds is estimated at less than 3.0 mW/m^2 (less than 1.0 TW) and that of the tides to be about 2.9 mW/m^2 (0.9 TW). The total mixing requirement in the ocean is estimated to be 9.3 mW/m^2 (2.9 TW; St. Laurent and Simmons, 2006). Thus, our

calculations, taken literally, suggest the biosphere can supply ~33% of the needed power. It is also possible to express bio-mixing in terms of diffusivities via the relation

$$\kappa = \frac{\varepsilon\Gamma}{N^2} = \frac{0.2 \ 1TW}{10^{-5} \ s^{-2}} : 2 \times 10^{-5} m^2/s \tag{7}$$

where the estimated biomixing input of 1 TW is assumed to be uniformly dissipated over the upper three km of the ocean. We have also used a buoyancy frequency of roughly $N^2 = 1$ cycle/30 min as an estimate of the average stratification; this is likely not an underestimate. The inferred diffusivity compares very favorably with the diffusivity measured in the upper thermocline by Ledwell *et al.* (1993).

Contributions to the dissipation from the winds and tides are by themselves enough to account for the observed diffusivity. All else aside, the diffusivity in (7) should be added to that from the winds and tides, and thereby elevate the gross diffusivity above the observed value. However, large, and unknown, error bars must be assigned to all these numbers, so we prefer not to accept them at face value. Instead, we suggest only that biosphere input to the mixing budget of the global open ocean appears to be substantial, and that there are reasons to believe it impacts mixing at the same level of importance as the winds and the tides. That the biosphere could have this large an impact on the climate system appears to have gone unnoticed. Further, the biosphere power supply estimated here exceeds the upper ocean 1.8 mW/m^2 (.64 TW) mixing consumption by a considerable amount (St. Laurent and Simmons, 2006). At an even more fundamental level, the biosphere emerges as a leading order contributor to the ocean energy budget. Of course, it contributes mostly in the form of chemical energy, thus operating like a battery.

The above argument has focussed on the mechanical energy, but it is interesting to recall that the part of the bio-energy flux not surrendered to mechanical energy enters the environment as heat. From the OUR rate of 20 TW, the implied thermal energy flux of 62 mW/m^2 (19 TW) is comparable to the geothermal heat flux through the ocean floor (104 mW/m^2; 32TW, Stein and Stein, 1992). While this is surprising, biomass heating of the ocean does not affect mixing because of the large heat capacity of water. The reasoning is the same as that in Huang (1999), who argued geothermal flux has a negligible effect on mixing.

a. Advantages

It is worthwhile to emphasize the attractive aspects of this suggestion, viz., ocean mixing. As mentioned, how effectively the power in the tides and winds mixes the aphotic ocean is unknown, primarily due to mismatches between the locations and spatial scales involved with their injection into the marine system. In contrast, the biosphere elegantly overcomes many of the related difficulties. The fish, whales, plankton, etc. involved transport energy directly to the depths involved by swimming there. The scales at which this energy enters the environment are close to the scales of mixing.

Munk (1966) considered the mixing impact of biological processes and concluded it was negligible. We find a different result here partly because we included the upper parts of the aphotic ocean where recently measured oxygen utilization rates are 30 times larger than the ~ 0.1 $\mu moleO_2 kg^{-1} yr^{-1}$ value he used. Also, oxygen utilization rate estimates have generally increased over the last few decades as improved measurement techniques have emerged (Jenkins, 1982;1987). Munk also ruled out zooplankton by arguing their deep biomass is small; we concur that migrating zooplankton are largely confined to the upper 1 km. Our calculations and Munk's (1966) overlap in the depth zone from roughly 1000 m to 2000 m and it is possible biosphere contributions beyond such depths are secondary.

b. Implications

It is fair to ask if biosphere mixing is significant to ocean climatology or heat flux. This question is motivated partly because the stratification of central interest in MW98 was that of the abyss, and intuitively one might expect most of the biosphere energy to be expended in the upper 1 km. A separate issue is the extent to which oceanic heat flux, particularly of the MOC, depends upon mixing. There are several arguments that can be raised with respect to both issues; we here emphasize two themes in order to suggest the question remains open. First, we reason that mixing from 500 m to 1500 m potentially plays an important circulation role. For example, Samelson and Vallis (1997) argue the wind-driven and overturning cells are joined by an internal boundary layer centered at, roughly, 1 km whose thickness is governed by mixing. This idea, in similar form, dates back to Stommel and Webster (1962) and, more recently, Young and Ierley (1986). Important water mass modifications are also known to occur in the upper 1 km in the Southern Ocean. Finally, Emanuel (2001) has argued for meridional heat flux sensitivity to mixing in the upper 500 m. His source for that mixing was tropical cyclones, but presumably the sensitivity would extend to other shallow energy inputs. Second, the objection that biosphere mixing enters dominantly in the upper 1 km could also be raised more forcefully with respect to wind input, all of which enters at the ocean surface. In comparison, a significant fraction of biosphere energy enters the marine environment at depths far closer to the locations of abyssal mixing than does the wind. Swimming, as a mechanism of vertical energy transport, is also clearly quite efficient, while the near inertial wind-energy suffers from weak vertical group velocities.

If the hypothesis offered here is valid, the aphotic marine biosphere impacts climate through its contribution to mixing and thus to the MOC. This biosphere/climate coupling is to our knowledge novel, and invites broad thinking about possible anthropogenic climate feedbacks. A decidedly speculative, and intentionally provocative, example involving overfishing appears in Appendix II.

5. Summary

Herein we have argued, or perhaps suggested, the biosphere contribution to aphotic ocean mixing is large. While we feel our approaches are straightforward and have obtained

comparable numbers when approaching the problem from several independent measurements, it would be naïve to assert we have found the right answer. In fact, we freely admit ours is an uncertain estimate and one where it is difficult to quantify error while allowing that they are large.

So, is there any validity to the idea offered here? As an overarching response, all of the bio-pathways flow from net primary production, *NPP*, and our estimate for *NPP* power, 62.7 TW, based in satellite observations calibrated against years of ground truth observations, is probably the soundest number in this paper. Of course, standing between this number and the real contribution are real pathways and mechanisms, of which some have here been described. But, all else aside, if only 1% of this energy (.63 TW) is available as aphotic mechanical energy, our point is made. The end result of our calculations is indeed a net transfer to mechanical mixing of approximately 1%. While it would be a remarkable feat if we were to be able to accurately estimate such a small transfer, it should be emphasized that the net effects of winds on mechanical energy in the open ocean are also currently estimated at comparable levels (i.e. <1 TW from a gross input of approximately 60 TW). Also, our relatively validated 17 GW toothed whale contribution mentioned at the beginning of our paper constitutes 2.5% of this goal while appealing to less than 0.5% of the total biomass in trophic levels 2-5 (i.e. 150 Mt of toothed whales in roughly 37 Gt of nonphytoplankton, nonbacterial marine biomass).

We have recently become aware of a highly relevant publication by Huntley and Zhou (2004). They estimate turbulence generation by schools of fish and conclude that the rates can be meaningfully compared to those caused by storms. Our approaches are very different and complementary, yet the conclusions are mutually supportive.

APPENDIX I

How much zooplankton biomass is there?

There is an interesting order of magnitude argument surrounding total zooplankton biomass, an ocean parameter that is not well known. Specifically, zooplankton biomass, or perhaps for this discussion trophic level 2 biomass, is related by gross ecological efficiency, f, to the biomass at higher trophic levels. In some ways, higher trophic level biomasses are better known than zooplankton biomass. So, for example, total sperm whale biomass is $M_{sw} = 14$ Mt (1 Mt $= 10^9$ kg), assuming a population of 360,000 at an average mass of 40 T. A rough estimate of the total trophic level 5 biomass, M_5, is somewhere

between $(20–100) M_{sw} = (300–1500)$Mt $= M_5$. Assume the former value as a conservative estimate. Zooplankton biomass, M_2 is related to M_5 according to $M_2 = f^{-3}M_5$. Gross ecological efficiency is itself not well known, but subject to some bounds. The classical value of f is 0.1, and values less than 0.06 are only infrequently observed in certain predator-prey subpopulations (Russell-Hunter, 1979). On the other hand, arguments are given that the theoretical maximum of f is $\sim.35$. If we assume 20% mass transfer efficiency between trophic levels, zooplankton biomass is $M_z = 30$ Gt (.1 kg/m^2), which is within observations, if on the high side (Blackburn, 1981). To lower zooplankton density requires increasing f, which given observed ranges is difficult to rationalize. Lowering transfer efficiencies to the more classical 10% implies an average 1 kg/m^2 zooplankton biomass density, which is higher than any open ocean observation. The upshots of this argument are simultaneously that 30 Gt (0.1 kg/m^2) zooplankton biomass is a reasonable number, and that gross ecological efficiencies are possibly higher than 0.1.

APPENDIX II

Is overfishing a mechanism of global climate change?

If the hypothesis offered here is valid, the aphotic marine biosphere impacts climate through its contribution to mixing and thus to the MOC. Should human interference in the climate be generalized to include overfishing?

Although we have argued the energy loss to fishing from the marine biosphere is relatively small, more telling measure for our present purposes is the potential *TMR* removed by the catch. Gross measures of trophic levels 2–5 *TMR* hover around 1 W/kg, thus the annual catch constitutes a removal from the biosphere mechanical energy budget of 17 GW/yr, based on an average 20% swimming efficiency. This probably implies 1–2 GW/yr loss for the aphotic ocean. If the extraction were claimed from 'elastic' marine species, i.e. those with high reproduction rates and relatively short lives, the loss would be rapidly replaced, and the effects minimal. But, the primary targets of human fishing are higher trophic levels, and many of the species are relatively 'inelastic,' i.e. have low reproduction rates and long lives and do not recover from increased harvesting. (Baum *et al.* (2003) speculate that ocean white-tip sharks, once among the most numerous of large animals on earth, are now extinct in the Gulf of Mexico.) In this case, potential *TMR* loss can, over time, add up. As a dramatic example, it is estimated that prewhaling sperm whale populations numbered 1.1 million (Whitehead, 2002), suggesting an anthropogenic drain of 700,000 animals. This constitutes a loss from the aphotic mechanical energy budget of 3.0 GW.

If we can ascribe a 500 GW loss to trophic levels 3–5, kinetic contributions break down across trophic levels roughly as 400, 80 and 16 GW, respectively, assuming a 20% transfer efficiency rate. Admittedly this is a higher transfer rate than the classical value of 10% but, as suggested in Appendix I, arguments can be made that 20% is not unreasonable. Many apex predator shark species are thought to currently inhabit the oceans at levels well less than half of their unfished populations (ICCAT, 2005). Other high trophic level species,

billfish for example, appear to have been drastically reduced in number in the latter half of the 20th century, based on measures like catches per 100 baited hooks (O'Dor, 2003). In view of this information, and assuming conservatively that levels 5 and 4 have been reduced in biomass by 50% and 20% respectively, 32 GW of mixing have been lost.

Like the CO_2 problem, however, many feedbacks are involved. For example, losing the high trophic levels might imply increased levels 2–3 biomass, and hence increases in zooplankton *TMR* work. Also, the photosynthesizers come under variable grazing pressure, thereby rocking the base of the pyramid. While it is fair to say the ultimate climate impact is unknown, the loss of 32 GW in mechanical energy due to human fishing can be compared to that which would result from the removal of the Hawaiian Islands, twice.

Of course, overfishing is far broader in its problematic impacts than this speculative one on climate; it is not our intent to unseat these often more immediate concerns.

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