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Prokaryotic responses to hydrostatic pressure in the ocean – a review

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Summary

Effects of hydrostatic pressure on pure cultures of prokaryotes have been studied extensively but impacts at the community level in the ocean are less well defined. Here we consider hydrostatic pressure effects on natural communities containing both unadapted (piezosensitive) prokaryotes originating from surface water and adapted (including piezophilic) prokaryotes from the deep sea. Results from experiments mimicking pressure changes experienced by particle-associated prokaryotes during their descent through the water column show that rates of degradation of organic matter (OM) by surface-originating microorganisms decrease with sinking. Analysis of a much larger data set shows that, under stratified conditions, deep-sea communities adapt to *in situ* conditions of high pressure, low temperature and low OM. Measurements made using decompressed samples and atmospheric pressure thus underestimate *in situ* activity. Exceptions leading to overestimates can be attributed to deep mixing events, large influxes of surface particles, or provision of excessive OM during experimentation. The sediment-water interface, where sinking particles accumulate, will be populated by a mixture of piezosensitive, piezotolerant and piezophilic prokaryotes, with piezophilic activity prevailing deeper within sediment. A schematic representation of how pressure shapes prokaryotic communities in the ocean is provided, allowing a reasonably accurate interpretation of the available activity measurements.

Introduction

Hydrostatic pressure influences the physiology of organisms living at depth in the ocean, the most extensive habitat of the biosphere in terms of volume (1.3 x 10^{18} m^3) (Whitman et al., 1998). The realm below 200 m, the dark ocean, is characterized not only by permanent darkness (insufficient light to support photosynthesis) but also by cold temperature (except for the Mediterranean, Red, and Sulu Seas), high inorganic nutrients, and low organic carbon concentration. Lauro and Bartlett (2007) described this physically uniform environment as being occasionally interrupted by outbursts of activity at sites of hydrothermal vents (Prieur et al., 1995), whale falls (Smith et al., 2003), cold seeps (Elvert et al., 2000), and deep hypersaline anoxic basins (van der Wielen et al., 2005; Daffonchio et al., 2006). In this review, organic aggregates and other anomalies in the water column are shown to have the capacity to interrupt this uniformity.

In the 1840s, the azoic-zone theory of Edwards Forbes prevailed, thus making presence of viable microorganisms in deep ocean water and sediment one of the first important discoveries in marine microbiology (Certes, 1884). ZoBell and Johnson (1949) began studies of the effect of hydrostatic pressure on microbial activity using pure cultures. “Barophilic” was the first term used to define optimal growth at a pressure higher than 0.1 MPa or for a requirement for increased pressure for growth (ZoBell and Johnson, 1949), but was subsequently replaced by Yayanos (1995), who suggested "piezophilic" (from the Greek “piezo”, meaning pressure). Current terminology (reviewed by Fang et al. 2010 and Kato 2011) defines pressure-adapted microorganisms either as piezotolerant (similar growth rate at atmospheric pressure and high pressure), piezophilic (more rapid growth at high pressure than atmospheric pressure), or

hyperpiezophilic (growth only at high pressure), with pressure maxima increasing in rank order (highest for hyperpiezophiles). Organisms that grow best at atmospheric pressure, with little to no growth at increased pressure, are termed piezosensitive.

Pressure-adapted microorganisms have been isolated from many deep-sea sites by researchers around the world. Isolates include representatives of the Archaea (both *Euryarchaea* and *Crenarchaea* kingdoms) mainly from deep-sea hydrothermal vents, and Bacteria from cold, deep-sea habitats. Most of the bacterial piezophiles have been identified as belonging to the genera *Carnobacterium, Colwellia, Desulfovibrio, Marinitoga, Moritella, Photobacterium, Pyschromonas*, and *Shewanella* (reviewed by Bartlett et al., 2007). The membrane properties of piezophiles have been described and other characteristics of piezophiles, including motility, nutrient transport, and DNA replication and translation under elevated hydrostatic pressure, have been explored (Lauro et al., 2008). Protein structural adaptation to high pressure has also been described in comparative studies of piezophilic and piezosensitive microorganisms (Kato et al., 2008).

Although the deep ocean supports a diversity of prokaryotes with functional attributes interpreted as adaptation to a pressurized environment (Lauro and Bartlett, 2007; Nagata et al., 2010), the contribution of the natural microbial assemblages to the carbon cycle of the biosphere remains poorly understood. Recent reviews (Arístegui et al., 2009; Nagata et al., 2010; Robinson et al., 2010) strongly suggest reconsidering the role of microorganisms in mineralizing organic matter in the deep pelagic ocean.

The deep-sea microbial food web is essentially dependent on particulate organic carbon (POC) flux from primary production in the euphotic zone, i.e., sunlit surface waters (Nagata et al., 2010). Recent discoveries challenge the paradigm that cycling of organic matter is slow in the

deep sea and mediated by microbial food webs of static structure and function. Data showing spatial variation in prokaryotic abundance and activity support the hypothesis that deep-sea microorganisms respond dynamically to variations in organic matter input to the bathypelagic realm (Nagata et al., 2010). About 30% and 19% of the water column-integrated prokaryotic heterotrophic production occurs in meso- and bathypelagic water, respectively, meaning that almost half of the total water column heterotrophic prokaryotic production takes place below the epipelagic layer (Arístegui et al., 2009). Over time, the deep ocean presumably exists in a steady state, with sources and sinks balanced. Recently compiled global budgets and intensive local field data suggest that the estimate of metabolic activity in the dark pelagic ocean exceeds the input of organic carbon (Burd et al., 2010). This imbalance indicates both existence of unaccounted sources of organic carbon (slowly degradable organic carbon, suspended organic matter, and *de novo* organic matter produced by dark CO_2 fixation) and overestimation of metabolic activity in the dark ocean. Budgets based on organic carbon flux and metabolic activity in the dark ocean are fraught with uncertainties, including environmental variability, measurement reliability, conversion accuracy, and insufficient sampling or estimation of key processes (Arístegui et al., 2009; Burd et al., 2010). In fact, rates of heterotrophic, prokaryotic biomass production and respiration are based on a relatively small data set and in many cases determined under atmospheric (sea surface) pressure.

Initial estimates of deep-sea microbial activity under elevated pressure were based on the unintentional experiment involving the "sandwich in the lunchbox" from the sunken research submarine Alvin, “incubated” *in situ* more than 10 months at 1540 m depth in the Atlantic Ocean (Jannasch et al., 1971). According to Jannasch et al. (1971), the crew’s lunch was recovered and “from general appearance, taste, smell, consistency, and preliminary biological and biochemical

assays, [...] was strikingly well preserved." Based on subsequent studies carried out employing *in situ* conditions of high pressure and low temperature, the Jannasch team concluded that deep-sea microorganisms were relatively inactive under *in situ* pressure and not adapted to high pressure and low temperature. However, Jannasch and Taylor (1984) offered the caveat that the type of substrate influenced the results and concluded, from laboratory experiments, that "barophilic growth characteristics have been unequivocally demonstrated". These early observations of deep-sea microbial activity were accompanied by development of pressure-retaining water samplers, with the conclusion from results of experiments employing these samplers that "elevated pressure decreases rates of growth and metabolism of natural microbial populations collected from surface waters as well as from the deep sea" (Jannasch and Wirsen, 1973). Contrary to this early conclusion, virtually all subsequently collected data from the water column under *in situ* conditions have shown that the situation is the reverse, namely those microorganisms autochthonous to depth are adapted to both the high pressure and low temperature of their environment.

In this review, we address the important point of microbial activity in the dark ocean and clarify the effect of hydrostatic pressure, focusing on origin of prokaryotes, i.e., surface-derived *versus* autochthonous deep-sea prokaryotes, and stratified *versus* mixed water conditions. We consider hydrostatic pressure effects in both the mesopelagic (depth range of 200–1000 m) and bathypelagic (1000–4000 m) realms and focus on results of experiments mimicking changes in pressure that prokaryotic communities experience in the water column when attached to sinking particles, during mixing, or undergoing deep-water convection. We also discuss results of *in situ* research whereby pressure (and temperature) of the deep sea are employed to evaluate adaptation of deep-sea prokaryotic assemblages to *in situ* conditions. By focusing on relative rates in the

literature, according to pressure during incubation, rather than absolute rates, we aim to inform experimental design and the achievement of more accurate estimates of microbial activity in the deep ocean.

Pressure effects on particle-attached prokaryotes sinking through the water column

Biogenic aggregates (> 500 µm in diameter), including marine snow and fast-sinking fecal pellets of large migrating macrozooplankton, constitute the majority of vertical particle flux to the deep ocean (Fowler and Knauer, 1986; Bochdansky et al., 2010). These aggregates can transport large numbers of attached prokaryotes to great depth (Turley and Mackie, 1995); e.g., 1.7 x 10^{10} bacteria g^{-1} fecal pellet at 4715 m (Deming, 1985). Enzymatic dissolution and mineralization of particulate organic matter (POM) by attached prokaryotes during descent can provide important carbon sources for free-living prokaryotes, thereby playing important biogeochemical roles in mesopelagic and bathypelagic carbon cycling (Cho and Azam, 1988; Smith et al., 1992; Turley and Mackie, 1994; Turley and Mackie, 1995). Attached prokaryotes, however, tend to comprise a small fraction (5%) of the total prokaryotic biomass (Cho and Azam, 1988), reaching somewhat higher proportions (10–34%) only when the concentration of aggregates is high (Turley and Mackie, 1995). Prokaryotic detachment from particles during rapid descent through the dark ocean would represent only a weak contribution to total prokaryotic biomass in deep waters (Turley and Mackie, 1994).

The extent to which sinking particles contribute to microbial community structure in the deep sea remains an open question. Relatively little information on phylogenetic diversity of particle-

associated and free-living microorganisms is available. Early phylogenetic analyses of particle-attached *versus* free-living prokaryotic assemblages in shallow waters revealed distinct communities associated with the two environments (DeLong et al., 1993; Crump et al., 1999). Results of molecular fingerprinting of microorganisms present in deeper mesopelagic water samples supported the 'generalist' hypothesis, in which a sizeable proportion of similar 'operational taxonomic units' are shared between both the attached and free-living fractions (Hollibaugh et al., 2000; Moeseneder et al., 2001; Ghiglione et al., 2007). Recent results obtained from a few samples collected at 6000 m (in the Puerto Rico Trench), however, suggest that exchange between the particles and surrounding water is limited. Indeed species richness estimates for Bacteria (though not Archaea) were much greater in the particle-associated fraction than the free-living fraction, including significant compositional differences (Eloe et al., 2011). The extent to which particle-associated prokaryotes contribute to structure of the surrounding community is a function of particle residence time (Kellogg and Deming, 2009), which can be expected to increase when there are mixing anomalies or in the benthic boundary layer of the deep sea.

In the early work on heterotrophic microbial activity associated with particulate matter in the deep sea, comparative responses to moderate (surface water) versus extreme (abyssal) temperatures and pressures were used to diagnose prokaryotic origin (Deming, 1985). Samples of sinking particulates, fecal pellets, and deposited sediments were collected in bottom-moored sediment traps and boxcores at station depths of 1850, 4120, and 4715 m in the North Atlantic and incubated for 2 to 7 days under both surface water and simulated deep-sea conditions (the latter in sterile syringes in pressure vessels at 3°C). In most cases, shallow water microbial activity was essentially predominant in sediment trap samples. However, microbial activity

associated with fecal pellets was increasingly piezophilic with increasing depth. In deposited sediments, the microbial response was always piezophilic. These results suggested that sinking POM, prior to burial in abyssal sediments, is altered by deep-sea pressure adapted prokaryotes, some of which are capable of surprisingly rapid activity at low temperature and elevated pressure (Deming, 1985).

To better understand the metabolic capacity of prokaryotes of shallow-water origin, that are carried below the euphotic zone on sinking particles, to degrade organic matter in the deep sea, different approaches proved informative. Turley (1993) applied increasing pressure to collections of sinking particles, obtained by trapping for 48 h at 200 m depth and containing microbial assemblages. These samples were placed in sealed bags incubated in pressure vessels at 5°C. Pressures of 0.1, 10, 20, 30 and 43 MPa were applied in step function (within 30 min, then maintained constant for 4 h), to simulate pressure at the deep sediment-water interface. Seawater samples collected at depths of 10 and 40 m were incubated under similar conditions, with microbial activity of both the seawater and sediment trap samples analyzed using leucine and thymidine incorporation. Results indicated that DNA and protein synthesis carried out by both free-living and particle-associated bacteria were significantly adversely affected by pressure (without loss in cell number). On the time scale employed in these experiments, it can be concluded that particle-associated bacteria from shallow water are unlikely to have a significant impact on degradation in the bathypelagic zone. In that zone, the activity of pressure-adapted bacteria, whether piezophilic or piezotolerant, are likely to have the greatest impact. Nevertheless, the observations of Turley (1993) help explain how labile organic matter associated with sinking particles can reach the seafloor with minimal degradation. This is consistent with the conclusion of Deming (1985) that degradation near and within the seabed is carried out by

pressure-adapted microorganisms. Both studies underscore pressure as an important factor constraining deep-sea carbon cycling that is not adequately appreciated.

To simulate more accurately the increase in pressure (and decrease in temperature) prokaryotes associated with particles experience in sinking to depth, Tamburini et al. (2009b) created a PArticulate Sinking Simulator (PASS) system. High-pressure bottles (HPBs) were used to incubate samples while pressure was increased continuously (linearly) by means of a piloted pressure generator. The HPBs were rotated (semi-revolution) to maintain particles in suspension during incubation in water baths reproducing temperature changes with depth. The PASS system can be used in the laboratory or at sea, depending on samples being analyzed and objectives of the study. Tamburini et al. (2006, 2009b) focused on prokaryotic processes and particle degradation in the mesopelagic zone, at the time just after particles exit the euphotic zone and before they arrive on the deep sea floor, employing a realistic settling velocity. The first such experiments used diatom detritus (*Thalassiosira weisflogii*) as particle source and was based on the experimental design of Bidle and Azam (1999, 2001) and Bidle et al. (2002, 2003), but modified to allow analysis of pressure effects on dissolution of biogenic silica and associated prokaryotic assemblages during simulated particle fall at a sinking rate of 150 m d^{-1} over eight days. The results indicated significantly lower (nearly 5-fold) aminopeptidase activity with increasing pressure, compared to constant atmospheric pressure which, in turn, limited biogenic silica dissolution to a simulated depth of 800 m (Tamburini et al., 2006). Although the rates decreased, in keeping with Turley (1993), phylogeny of the prokaryotic assemblages changed little during this simulated sinking event.

In another set of PASS experiments, using freshly recovered particulate matter, the change under *in situ* hydrostatic pressure that particles experience when sinking (200 m d^{-1}) from

mesopelagic to bathypelagic depths was simulated. The concentration (normalized to POC) of particulate chloropigment, carbohydrate and transparent exopolymer particles decreased both under increasing pressure and at atmospheric pressure. However, less degradation occurred under increasing pressure. Dissolved carbohydrate (normalized to DOC) increased under both sets of conditions, but more so under atmospheric pressure. In any case, these results indicate production by microorganisms associated with the particulate fraction. Particulate wax/steryl esters (normalized to POC) increased only under pressure, suggesting metabolic response of the prokaryotes to increasing pressure. After incubation, Bacteria dominated (~ 90%) the prokaryotic community, with *Gammaproteobacteria* comprising the largest fraction, followed by *Cytophaga–Flavobacter-Bacteroides* and *Alphaproteobacteria*. Tamburini et al. (2009b) hypothesized that *Cytophaga-Flavobacter-Bacteroides* are more sensitive to elevated pressure, hydrolyzing less particulate carbohydrate and thereby limiting the dissolved carbohydrate available to metabolism by *Alphaproteobacteria* and explaining the lower abundance of these organisms under increasing pressure. The Archaea played a less significant role in degradation of particulate organic matter (Bidle and Azam, 2001; Simon et al., 2002; Tamburini et al., 2006), and they did not increase in number on the particles in surface water (Simon et al., 2002). Exceptions have been observed in river-impacted seas, where nepheloid (particle-rich) layers advecting offshore contained elevated concentrations of Archaea (Wells and Deming, 2003) and aggregates supported archaeal communities phylogenetically distinct from their free-living counterparts (Kellogg and Deming, 2009). PASS experiments have also shown that detritus-associated Archaea will decrease rapidly upon pressurization (Tamburini et al., 2006), suggesting that the large number of free-living Archaea in the deep sea (DeLong et al., 1999; Karner et al., 2001; Church et al., 2003; Teira et al., 2004; Herndl et al., 2005; Tamburini et al., 2009a) is not explained by vertical transport of

sinking particles. Again using the PASS system, Tamburini et al. (2006, 2009b) obtained chemical and microbial evidence that OM degradation by prokaryotes associated with particulate material sinking through mesopelagic waters is limited by increasing pressure.

An approach to measuring pressure-induced microbial succession on sinking particles was developed by Grossart and Gust (2009). They used a computer-controlled pressure system in the laboratory to simulate sinking at 1000 m d^{-1}, i.e., from surface to 4000 m in an isothermal ocean. Instead of natural communities, they tracked a mixture of five bacterial strains, isolated from aggregates in surface water and belonging to different taxa [*Cytophaga*, *Gammaproteobacteria*, *Bacillus*, *Alphaproteobacteria* (non-*Roseobacter* and *Roseobacter*)]. These results must be interpreted with caution, because the cultures and system were artificially enriched (Marine Broth) and incubation was conducted at a constant temperature of 20.5°C even as pressure was increased (an unrealistic ocean). Nevertheless, the approach itself is promising as a method for monitoring microbial community response to pressure, especially since some strains (*Bacteroides* and *Bacillus*) were reported to grow only at moderate pressures, i.e., up to 15 MPa, while others (non-*Roseobacter* and *Gammaproteobacteria*) grew at pressure of at least 40 MPa, suggesting pressure-induced succession may occur.

The origin, i.e., surface versus depth, and role of prokaryotes in the deep sea were recently addressed by Egan et al. (2012) using seawater samples collected from a depth of 3170 m in the NE Atlantic Ocean. Shifts in bacterial community structure were evaluated according to incubation pressure (atmospheric *versus* 31 MPa), using *in situ* deep-sea temperature (4°C) and the same artificial nutrient enrichment in each case. The behavior (fitness) of individual community members (Operational Taxonomic Units: OTUs) was determined before and after incubation for one month using denaturing gel gradient electrophoresis (DGGE) of the 16S rRNA

gene (rDNA). Of the resulting sequenced DGGE bands, 70% scored as OTUs favored by one set of conditions or another (atmospheric or *in situ* pressure). Six of the OTUs were classified as autochthonous, i.e., adapted to *in situ* pressure. Nine of the OTUs were concluded to be surface-derived allochthonous microorganisms (not adapted or native to deep-sea conditions). *Gammaproteobacteria* and, to a lesser extent, *Cytophaga–Flavobacterium–Bacteroides* and *Deltaproteobacteria* sequences dominated regardless of treatment. The results of Egan et al. (2012) provide useful phylogenetic data that support the hypothesis developed over the past several decades (Deming, 1985; Turley, 1993; Tamburini et al., 2009b) that surface-derived Bacteria reach the deep sea but most of the carbon cycling in the deep sea is accomplished at depth by pressure-adapted and/or piezophilic microorganisms. Archaea, which represent a significant fraction of prokaryotic communities of the deep ocean (Karner et al., 2001; Church et al., 2003; Teira et al., 2004; Herndl et al., 2005; Tamburini et al., 2009a), have not been similarly studied.

In summary, the effect of pressure on surface-derived Bacteria attached to sinking organic matter is that their contribution to decomposition and dissolution of organic matter decreases with depth. This reinforces the conclusion that rapidly settling particles are less degraded during passage through the mesopelagic water column and, therefore, this phenomenon results in a labile food supply for bathypelagic and epibenthic communities (Honjo et al., 1982; Turley, 1993; Wakeham and Lee, 1993; Goutx et al., 2007). It also fits the results of *in situ* experimentation (Witte et al., 2003) and the calculation of recently proposed models (Rowe and Deming, 2011) that show effective competition between metazoa and microorganisms for resources reaching the deep seafloor from the sea surface.

Comparative effects of *in situ* high versus low pressure on deep-sea prokaryotic communities

Microbiology of the deep realm is limited by both the expense of the equipment and time involved in sampling remote parts of the ocean. Remotely operated vehicles (ROVs) and human occupied submersibles have provided an extraordinary capability for deep-sea microbiology but, for the most part, have been employed to investigate hydrothermal vents, with stunning success. Nevertheless, most marine microbiologists do not have access either to an ROV or submersible, or even to pressure-retaining samplers. Thus, decompressed samples brought on board oceanographic ships are subjected to rapid recompression in order to reinstitute *in situ* conditions. Stainless steel pressure vessels are most commonly employed (reviewed by Deming, 2007). This method has been used to study sediment samples or samples collected at the sediment-water interface (see Table S1), as well as to isolate piezophilic deep-sea strains and bring them into culture. When temperature is held stable after collection, many bacterial isolates can survive and adjust to less drastic changes in pressure (ZoBell, 1970; Deming, 1993). Yayanos and DeLong (1987) and Deming et al. (1988) showed that the rate of cell division of obligatory piezophilic bacterial strains cultivated under copiotrophic conditions is not altered by repeated (brief) compression-decompression sequences. However, Bianchi and Garcin (1993) showed that, under oligotrophic conditions, the metabolic rate of deep-water microbial populations that have been decompressed during retrieval and then recompressed is clearly lower than that of their undecompressed counterparts. The effect of successive pressure shock on the metabolic rate of natural microbial populations has yet to be fully described.

A limited number of high-pressure vessels have been constructed during the past 50 years to measure microbial activity in the cold deep ocean and evaluate the effects of hydrostatic pressure,

as well as decompression, on deep-sea microbial activity. Sterilizable pressure-retaining samplers for retrieving and sub-sampling undecompressed deep-sea water samples have been developed independently by three laboratories including Jannasch/Wirsen at the Woods Hole Oceanographic Institution (USA), Colwell/Tabor/Deming at the University of Maryland (USA), and Bianchi at the Aix-Marseille University (Marseille, France) (Jannasch and Wirsen, 1973; Jannasch et al., 1973; Tabor and Colwell, 1976; Jannasch and Wirsen, 1977; Deming et al., 1980; Bianchi and Garcin, 1993; Bianchi et al., 1999a; Tholosan et al., 1999; Tamburini et al., 2003). Extensive sampling equipment for cold deep-sea high pressure work has also been developed by Horikoshi and his team (Jamstec, Japan) exclusively devoted to recovering new piezophilic microorganisms and to study the effect of pressure on those isolates, as described in the Extremophiles Handbook (Horikoshi, 2011). At least two other groups are developing pressure-retaining samplers, the Royal Netherlands Institute for Sea Research (NIOZ) and the National University of Ireland (Galway), but the designs or initial results have not yet been published.

To evaluate the state of the field of piezomicrobiology, we have compiled data from published studies of deep samples where prokaryotic activities were measured under conditions of *in situ* pressure and the results compared with those obtained using incubation at atmospheric pressure after decompression (Table S1). Sampling site, depth at which samples were collected, nature and concentration of substrate, incubation time, metabolic process studied (assimilation and respiration of monomers – or more complex substrates, prokaryotic heterotrophic production, and ectoenzymatic activity), and activity values obtained under elevated (*in situ*) pressure (HP), with the decompressed (DEC) sample aliquot incubated at atmospheric pressure. Samples are identified according to hydrological conditions (e.g., mixed water versus stratified water). Some samples were collected at sites where swarms of fecal pellets from migrating zooplankton were

present. Other samples collected from near bottom water, sediment contact water, and different strata within sediment samples are also listed. We have calculated, when feasible, the pressure effect (Pe), defined as the ratio between activity obtained under HP and that obtained under DEC conditions (Pe = HP/DEC), where a ratio > 1 indicates piezophily (adaptation to high pressure) and a ratio < 1, piezosensitivity. The literature citation for each value is given. Finally, to serve as comparative or "negative" controls, we assembled published data on microbial rates determined in shallow water samples (≤ 200 m), incubated at both atmospheric and deep-sea pressure (Table S2), and calculated the associated Pe values (Pe = HP/ATM).

As stated above, the first report of deep-sea microbial activity measured without change from the *in situ* pressure was published by Jannasch and Wirsen (1973), who concluded that elevated pressure causes a decrease in rate of growth and metabolism of natural microbial populations collected from both surface water and the deep sea. As pointed out earlier, this conclusion has not stood the test of time, based on data in the literature and calculation of Pe values as shown in Table S1. Of the total Pe values calculated (n = 252), the majority (76%) were greater than 1, indicating some form of adapting to pressure. Piezosensitivity or pressure inhibition (n = 60 for Pe < 1) was indicated in approximately 40% of the samples for which data were generated in the early work of Jannasch's laboratory. Labeled substrates were added to samples collected at the sediment-water interface, the arrival point of sinking particles, involved at concentrations between 30 and ~ 300 μM, well above those in deep-sea water where concentrations of organic matter are low. Also, the endpoint incubation periods were unequal (several weeks for HP samples, compared to a few days for DEC samples), precluding calculation of first-order rates (Table S1). However, the effect of increased pressure on metabolic rate is, indeed, substrate-dependent, as shown by Jannasch and Taylor (1984).

Calculation of Pe values (Table S1) has proven to be a useful diagnostic tool for evaluating the effect of decompression on metabolic rate in deep-sea samples. A Pe ratio > 1 indicates the deep-sea prokaryotic assemblage is adapted to predominantly the *in situ* pressure and prokaryotic activity will be underestimated if the sample is decompressed and incubated at atmospheric pressure. On the other hand, if the Pe < 1, inhibition by high pressure is indicated and metabolic activity will be overestimated if the sample is decompressed. Figure 1a illustrates distribution of Pe values for the entire set of data on deep-sea samples shown in Table S1 (n = 252), along with values for shallow water or "negative control" samples (n = 30; Table S2). As expected, the latter samples yielded values < 1, indicating piezosensitivity, with the single exception of a sample from 200-m depth indicating piezotolerance (Pe = 1; Table 1). In contrast, the median Pe value for the deep samples was calculated to be 1.58 and mean 3.00 ± 0.40 (± s.e.), with 50% of the values distributed between 1.00 and 2.32 (Table 1). A maximum value of 61.5 was calculated from microbial production measurements for deep stratified water (Poremba, 1994), while a minimum of 0.01 was calculated from Jannasch and Wirsen (1973). To constrain distribution, the Pe values were categorized according to nature of the sample (see descriptive statistics in Table 1). The three major sample categories were deep-sea water collected during stratified conditions (n = 120), sediment (n = 71), and near bottom water (NBW) and deep-sea sediment contact water (SCW) (NBW + SCW, n = 23). Three other categories with fewer observations were differentiated (Table 1): water samples collected during a mixing event (n = 8) as described by Bianchi and Garcin (1994) and Boutrif (2012); samples of a swarm of fecal pellets discharged by migrating zooplankton (n = 8) as described by Bianchi et al. (1999b); and samples collected from deep hypersaline anoxic basins of the Eastern Mediterranean Sea (DHABs, n = 6) as described by

Tamburini (2002). When the nature of a sample was not indicated by the cited reference, the Pe was classified as NI (n = 27).

Figure 1b shows the distribution of Pe values for the three major categories of deep-sea samples described above. The mean Pe (n = 120) for stratified water was 4.01 (median 2.11), with 50% of values between 1.50 and 2.82 and 90% between 1.12 and 8.17 (Fig. 1b). During stratified conditions, the prokaryotic assemblage was adapted to high pressure (Wilcoxon rank test Pe > 1, $p < 2.2 \times 10^{-16}$) and the metabolic rate has to be determined under *in situ* pressure conditions to avoid underestimating activity. For sediment, the mean Pe was lower, at 1.59 (n = 71) and closer to the median of 1.40. Box plots of the data (Fig. 1b) show that if 50% of the Pe values are above 1, the lower bar crosses Pe = 1. However, sediment samples, when decompressed and recompressed to *in situ* pressure, appear to be significantly piezophilic (Wilcoxon rank test Pe > 1, $p = 1.143 \times 10^{-8}$). In contrast, near bottom and sediment contact water samples showed the opposite (Wilcoxon rank test Pe > 1, p = 0.1996). Although the mean Pe was 1.93 (n = 23), the median (less influenced by extreme values) approached 1 and the box plot crosses the Pe = 1 line (Fig. 1b). For near bottom and sediment-water interface samples, the arrival point of sinking particles, this interface can be considered a “mixing bowl,” with both autochthonous deep-sea microorganisms and allochthonous surface organisms that had colonized sinking particles from the surface (Deming, 1985). The former population functions well under ambient high pressure, while the latter does not and is inhibited by deep-sea conditions (Jannasch and Wirsen, 1973; Turley and Lochte, 1990; Turley, 1993; Bianchi and Garcin, 1994), as indicated by the low (< 1) Pe values for shallow water samples (Fig. 1a).

Although the data sets were too small for statistical analysis, the Pe values calculated for samples collected from a swarm of fecal pellets discharged by migrating zooplankton (Fecal

pellets, n = 4), during mixed water conditions (Mixed, n = 8), and from deep hypersaline anoxic basins (DHABs, n = 6) are instructive (Tables 1 and S1). The first two represent surface-derived prokaryotes rapidly transferred to depth, with Pe < 1 including the mean and median values for both data sets. These prokaryotic communities were inhibited by high pressure and weakly active at depth. With decompression, metabolism and growth were enhanced. The third case, deep hypersaline anoxic basins, provides a clear observation of adaptation to the pressure of an extreme environment. All metabolic rates were higher in samples incubated under high pressure, compared to those for samples decompressed during retrieval (mean Pe = 11.9, median = 3.4, n = 6). These data suggest the populations were adapted to the deep hypersaline anoxic environment. Metagenomic analysis will surely provide useful genomic information concerning the associated microbial assemblages and their function in the deep sea.

Conclusion

A schematic model of the effect of pressure on microbial populations according to origin (surface water versus deep sea) and fate is presented in Figure 2. Microbial communities found in the deep ocean comprise those microorganisms autochthonous to the deep sea and adapted by some degree to *in situ* temperature and pressure of the deep-sea environment and allochthonous microorganisms transported from the sea surface via sedimenting particles, deep migrating zooplankton or other mechanisms. Metabolic activity of an allochthonous community decreases with depth, limiting its capacity to degrade organic matter sinking through the water column (Turley, 1993; Turley et al., 1995; Tamburini et al., 2006). Such microbial communities may be inactive (not dead) under conditions of low temperature and elevated pressure of the deep sea, but

they can become dominant, i.e., more numerous and metabolically active when incubated under atmospheric pressure. Thus, community activity measured at atmospheric versus deep-sea pressure can reflect an entirely different mixture of community components.

Under conditions of elevated pressure and low temperature, microorganisms in the bathypelagic ocean can metabolize complex mixtures of organic matter and respond to changes in the biogeochemical state of the ocean (Nagata et al., 2010). The conceptual framework of the "microbial carbon pump" includes microbial production of recalcitrant dissolved organic matter and, thus, a mechanism for long term carbon storage (Jiao et al., 2010). Related arguments have been made for the contribution of microbial communities in deep-sea sediment to carbon storage (Rowe and Deming, 2011). Clues from genomic and transcriptomic analysis (Vezzi et al., 2005; DeLong et al., 2006), as well as measurement of degradation of refractory organic matter in deep water compared to surface water (Hoppe and Ullrich, 1999; Teira et al., 2006; Tamburini et al., 2009a; Boutrif et al., 2011), indicate that organic compounds resistant to microbial degradation at one depth horizon can serve as substrate for populations of heterotrophic microbes at greater depths (Carlson et al., 2011).

The response of deep-sea microbial lineages to exported DOC indicates that microbial processes carried out in the deep ocean include metabolism of persistent polymeric compounds. Genomic and transcriptomic data indicate the potential of marine bacterioplankton to utilize a range of DOM (Kujawinski, 2011; Giovannoni and Stingl, 2005; McCarren et al., 2011). For example, a large number of genes putatively involved in polysaccharide degradation has been identified in deep sea microbial populations compared to surface populations (DeLong et al., 2006). When isolated in culture, piezophiles can degrade complex organic matter (Vezzi et al., 2005) by modifying gene expression and protein regulation (Lauro and Bartlett, 2007). A good

example is that of the metabolic pathways employed by *Photobacterium profundum* to degrade polymers, such as chitin, pullulan, and cellulose, controlled by pressure, with up-regulation of proteins occurring above 28 MPa and down-regulation below 0.1 MPa. In the NW Mediterranean Sea, Boutrif et al. (2011) discovered natural assemblages that under *in situ* pressure and temperature (conditions of the deep sea) could degrade semi-labile exopolysaccharides (^{3}H-EPS). They observed higher cell-specific assimilation of ^{3}H-EPS by the deep sea prokaryotes compared to microbial communities in the surface water. Euryarchaea were identified as the main contributor to ^{3}H-EPS assimilation under *in situ* conditions, i.e., those found at a depth of 2000 m. Perhaps the best example of *in situ* microbial degradation of unusual organic compounds comes from another "unintended experiment," namely that of the Deepwater Horizon oil spill, where a deep-water plume of hydrocarbons triggered significant *in situ* microbial response, in the form of a bloom of members of the genus *Colwellia* originally described by its pressure adaptation (Deming et al., 1988). Members of the genus *Cycloclasticus* previously studied only in shallow waters were also dominant in the plume of the hydrocarbon from the spill (Valentine et al., 2011).

In conclusion, microbial metabolic rates are best measured under *in situ* conditions, which in the case of deep-sea microbial populations include high pressure, low temperature, and appropriate concentration (usually low) of ambient nutrient. An improved understanding of the biogeochemical roles of microorganisms in the deep sea will come from an expansion of studies that couple gene-based analyses with pressure incubations to measure microbial activity; e.g., microautoradiography coupled with in situ hybridization techniques under deep-sea conditions. Further application of "omic" approaches (genomic, transcriptomic, metabolomic) to the bathypelagic realm will reveal both metabolic potential and activity in powerful ways if the

critical factor of pressure is accommodated. New and improved methods are needed to measure the rate of enzymatic degradation of semi-labile and refractory organic matter and of microbial respiration in the deep sea, parameters crucial to a quantitative resolution of carbon fluxes as altered by prokaryotes (Burd, 2010). Although we have focused on physical (high pressure) control of microbial activity in the deep sea, biological controls (viruses [Danovaro et al. 2008] and other components of the microbial loop) also merit further study. Finally, recent highlights of possible chemolithoautotrophy in the dark realm (Herndl et al., 2005; Swan et al., 2011; Wuchter et al., 2006) stress the need for knowledge of chemolithoautotrophic activity (gas-consuming as well as gas-producing) under *in situ* conditions. Methanotrophy in cold deep water has already been identified as inherently piezophilic (de Angelis et al., 1991), based not only results of comparative pressure incubations, as emphasized in this review, but also on the fact that cold fluid under high pressure contains higher gas concentration than warmer or decompressed fluid. Recent events suggest urgency to understanding pressure effects on methane and other gas-dependent microorganisms in the deep sea, where they appear to be serving as effective biofilters (Kessler et al. 2012) against the release of potent greenhouse gases from the ocean.

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Figure captions

Figure 1: Box-and-Whisker plot of pressure effect (Pe) (a) based on the entire data set of calculated Pe values for deep samples (All; Table S1), as well as for shallow water controls (Surface; Table S2), and (b) according to the nature of the deep samples (Table S1). Pe is the ratio of rate measured under *in situ* pressure and rate measured after decompression and incubation at atmospheric pressure. Deep samples were collected from stratified water (Stratified water); sediment (Sediment); and near bottom water and sediment contact water (NBW+SCW). The top and bottom of each boxplot represent 75% and 25% of all values, respectively, the horizontal line is the median, and the lower and upper bars represent 10% and 90% limits, respectively. Outliers are shown as black dots.

Figure 2: Schematic representation of prokaryotic response to high-pressure conditions in diverse marine environments and estimation of the subsequent effect of sample decompression and/or incubation at 0.1 MPa (atmospheric pressure) on prokaryotic activity. From left to right, diverse conditions include: particles sinking through the water column; mixing conditions during winter or deep water convection from surface to deep; and stratified water. A-sP: attached surface prokaryotes (piezosensitive); FL-sP: free-living surface prokaryotes (piezosensitive); FL-dsP: free-living deep-sea prokaryotes (piezophilic); Sed-dsP: prokaryotes from the sediments (piezophilic).

Table 1. Descriptive statistical analyses of pressure effect (Pe), with values according to nature of the sample. Surface = shallow water samples subjected to an increase in pressure (described in Table S2). All deep data = entire data set obtained from deep samples (described in Table S1). Stratified water = samples obtained during stratified water conditions; Sediment = samples obtained from different strata of the sediment; NBW + SCW = samples obtained from near bottom water and sediment contact water; NI = hydrological conditions not indicated in the cited reference (Table S1); DHABs = samples from deep hypersaline anoxic basins; Fecal pellets = samples from a swarm of fecal pellets discharged by migrating zooplankton; Mixed = samples obtained during mixed water conditions.

	Surface	All deep data	Stratified water	Sediments	NBW+SCW	NI	DHABs	Fecal pellets	Mixed
No. of observations	30	252	120	71	23	27	6	4	8
Minimum	0.01	0.01	0.60	0.14	0.06	0.01	1.56	0.90	0.03
Maximum	1.0	61.5	61.5	6.9	7.6	38.0	56.9	1.10	1.78
1st Quartile	0.13	1.00	1.50	1.00	0.80	0.35	2.13	0.90	0.70
Median	0.22	1.58	2.11	1.40	1.09	0.48	3.41	0.90	0.99
3rd Quartile	0.39	2.32	2.82	1.95	1.97	1.00	4.15	0.95	1.26
Mean	0.29	3.00	4.01	1.59	1.93	2.19	11.89	0.95	0.98
Standard deviation	0.05	6.40	6.83	0.99	2.02	7.20	22.06	0.10	0.59
Standard error	0.23	0.40	0.62	0.12	0.42	1.39	9.01	0.05	0.21
Interval of confidence (95%)	0.04	0.79	1.22	0.23	0.83	2.72	17.65	0.10	0.41
No. of observations < 1	29	60	8	16	9	20	0	3	4
Percent of observations < 1	97	24	7	23	39	74	0	75	50

Table S1. Pressure effect on microbial activity measurements for deep-sea samples incubated under both ambient (high) and atmospheric pressure, compiled from the literature.

HP = rate measured on samples under ambient high pressure (value ± SE); DEC = rate measured on decompressed counterparts incubated at atmospheric pressure (value ± SE).

a = in situ incubation in sampler at the sampling-depth pressure during the entire incubation

b = in situ incubation at the sediment-water boundary layer using man-operated submersible

c = calculated by applying a factor of 12 to % utilization measured under atmospheric pressure for a 1-month period

d = sample incubated in the transfer unit for 45 days before transfer to the culture vessel, at the start of the incubation period

e = data originally presented as graphs of time-course incorporation, or respiration, of added substrate

f = within the set of data presented, the authors note that most experiments were conducted immediately after sampling, but some used undecompressed and concentrated subsamples kept in cold storage for an undetermined period before processing in the laboratory onshore. Authors did not indicate which samples were analyzed after storage under high pressure conditions.

g = set of six samples collected 30 nautical miles southeast of Marseille at the same sampling station and depth (reported data are mean value ± SD)

h = set of samples collected 28 nautical miles south of Nice in the Ligurian Sea at the same sampling station and depth during different water conditions (n = 8 for stratified, n = 3 for mixed); rate is mean ± SD

i = set of samples collected 28 nautical miles south of Nice in the Ligurian Sea at the same sampling station and depth over a few days, with some including a swarm of fecal pellets discharged by migrating zooplankton

REC = Decompressed then recompressed under in situ pressure conditions

NI = not indicated in the cited reference

ND = not determined by authors reporting the original data

H_r = Hydrolysis rate constant (see Tamburini et al. 2002 for details)

V_{max} = maximum velocity

Table S2. Pressure effect on microbial activity measurements for shallow-water samples incubated under both atmospheric and higher pressures, compiled from the literature.

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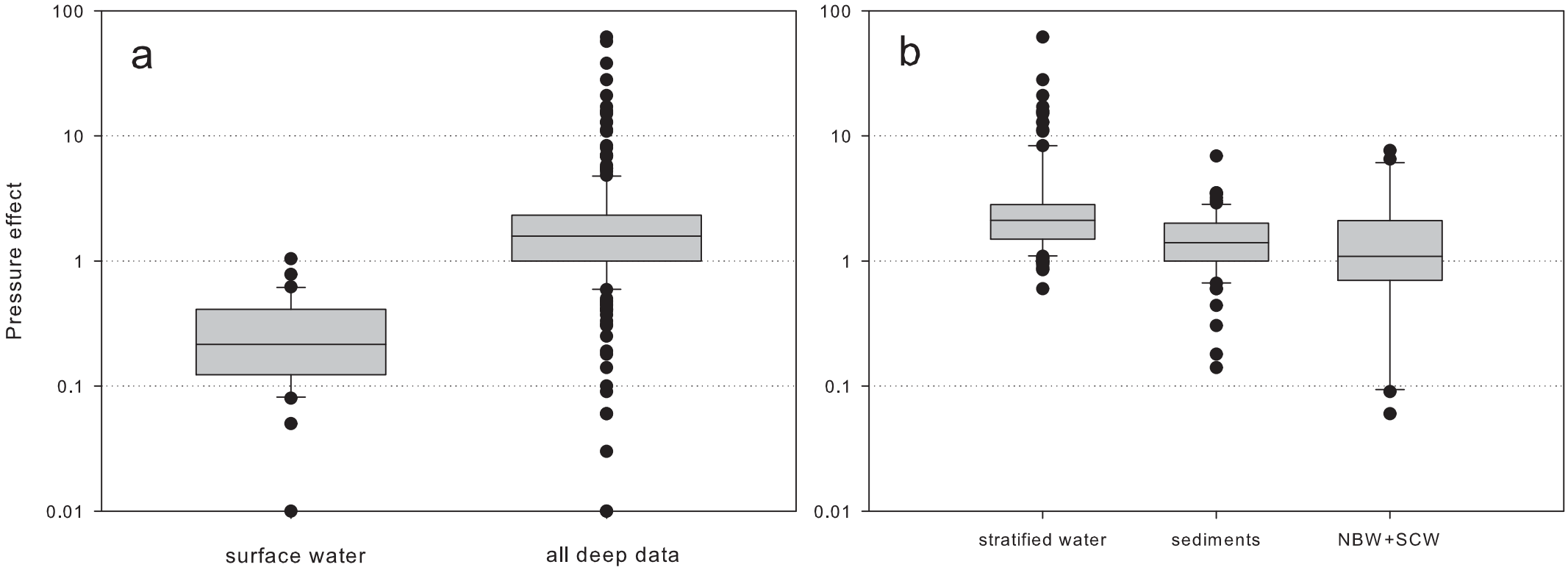
a
b
Pressure effect
100
10
1
0.1
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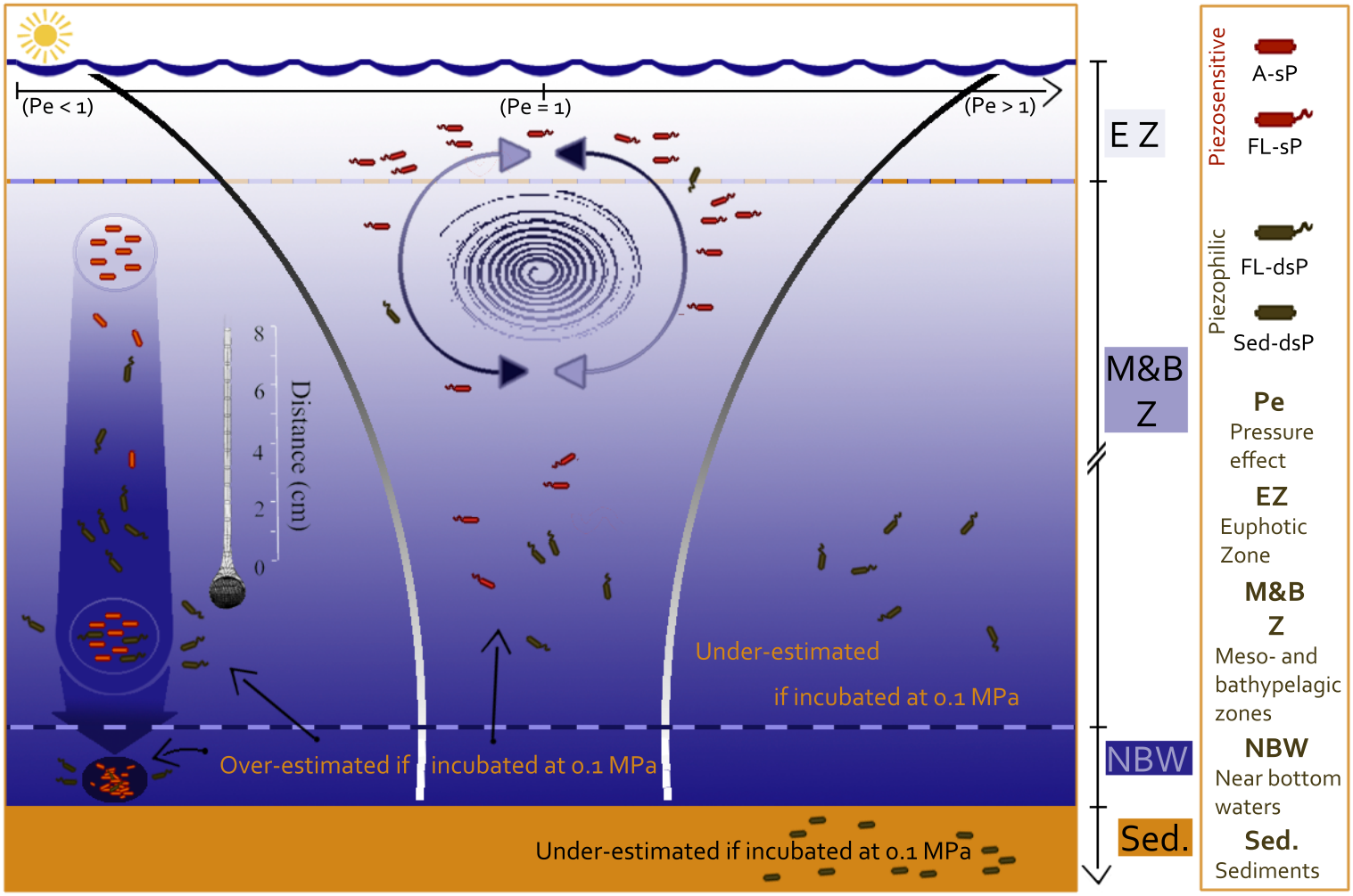
surface water
all deep data
stratified water
sediments
NBW+SCW


(Pe < 1)
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(Pe > 1)
E Z
M&B Z
NBW
Sed.
Distance (cm)
8
6
4
2
0
Under-estimated
if incubated at 0.1 MPa
Over-estimated if incubated at 0.1 MPa
Under-estimated if incubated at 0.1 MPa
Piezosensitive
A-sP
FL-sP
Piezophilic
FL-dsP
Sed-dsP
Pe
Pressure effect
EZ
Euphotic Zone
M&B Z
Meso- and bathypelagic zones
NBW
Near bottom waters
Sed.
Sediments

Table S1. Pressure effect on microbial activity measurements for deep-Sea samples incubated under both ambient (high) and atmospheric pressure, compiled from the literature.

HP = rate measured on samples under ambient high pressure (value ± SE); DEC = rate measured on decompressed counterparts incubated at atmospheric pressure (value ± SE).
a = in situ incubation in sampler at the sampling-depth pressure during the entire incubation
b = in situ incubation at the sediment-water boundary layer using man-operated submersible
c = calculated by applying a factor of 12 to % utilization measured under atmospheric pressure for a 1-month period
d = sample incubated in the transfer unit for 45 days before transfer to the culture vessel, at the start of the incubation period
e = data originally presented as graphs of time-course incorporation, or respiration, of added substrate
f = within the set of data presented, the authors note that most experiments were conducted immediately after sampling, but some used undecompressed and concentrated subsamples kept in cold storage for an undetermined period before processing in the laboratory onshore. Authors did not indicate which samples were
g = set of six samples collected 30 nautical miles southeast of Marseille at the same sampling station and depth (reported data are mean value ± SD)
h = set of samples collected 28 nautical miles south of Nice in the Ligurian Sea at the same sampling station and depth during different water conditions (n = 8 for stratified, n = 3 for mixed); rate is mean ± SD.
i = set of samples collected 28 nautical miles south of Nice in the Ligurian Sea at the same sampling station and depth over a few days, with some including a swarm of fecal pellets discharged by migrating zooplankton
REC = Decompressed then recompressed under in situ pressure conditions
NI = not indicated in the cited reference
ND = not determined by authors reporting the original data
H_r = Hydrolysis rate constant (see Tamburini et al. 2002 for details)
V_{max} = maximum velocity

Sampling area	Depth (m)	Added substrate	Concentration	Incubation period	Metabolic process	Ambient pressure (HP)	Atmospheric pressure (ATM)	Nature of the samples	Pressure effect	Reference	
N Pacific coast	400 (a)	^{14}C-glucose	250 µg l^{-1}	4 hours	substrate uptake	NI	NI	NI	1.66	Seki & Robinson (1969)	
NW Atlantic	1830 (b)	Starch	1.0 g l^{-1}	HP: 1 year / ATM: 1 month	% of substrate utilization	11.0 % (1 year)	16.0 % (1 month) (c)	NI - sediment contact water	0.06	Jannasch & Wirsen (1973)	(c)
NW Atlantic	1830 (b)	Agar	0.3 g l^{-1}	HP: 1 year / ATM: 1 month	% of substrate utilization	1.5 % (1 year)	13.0 % (1 month)	NI - sediment contact water	0.01	Jannasch & Wirsen (1973)	(c)
NW Atlantic	1830 (b)	Gelatin	1.0 g l^{-1}	HP: 1 year / ATM: 1 month	% of substrate utilization	4.85 % (1 year)	50.3 % (1 month)	NI - sediment contact water	0.01	Jannasch & Wirsen (1973)	(c)
Bermuda area	1800	^{14}C-glutamate	34 µM	9 days	% of substrate utilization	ND	ND	NI	0.25	Jannasch et al. (1976)	
Bermuda area	3000	^{14}C-glutamate	34 µM	16 days	% of substrate utilization	ND	ND	NI	0.33	Jannasch et al. (1976)	
Bermuda area	3130	^{14}C-casamino acids	5 mg l^{-1}	6 days	% of substrate utilization	ND	ND	NI	0.47	Jannasch et al. (1976)	
NW Atlantic	2600	^{14}C-casamino acids	5 mg l^{-1}	8 days (d)	total substrate utilization	ND (e)	ND (e)	NI	0.4	Jannasch & Wirsen (1977)	(d)
Puerto Rico Trench	3450	^{14}C-glutamate	0.82 µM	161 days	% of substrate utilization	0.046	ND	NI	ND	Deming et al. (1980)	
Gillis Deep	6040	^{14}C-amino acids	1.10 µM	43 days	% of substrate utilization	0.025	ND	NI	ND	Deming et al. (1980)	
Gillis Deep	6040	^{14}C-glutamate	1.22 µM	326 days	% of substrate utilization	0.058	ND	NI	ND	Deming et al. (1980)	
Brownson Deep	7730	^{14}C-glutamate	3.40 µM	159 days	% of substrate utilization	0.206	ND	NI	ND	Deming et al. (1980)	
Puerto Rico Trench	7350	^{14}C-glutamate	1.22 µM	48 days	% of substrate utilization	0.259	ND	NI	ND	Deming et al. (1980)	
NW Atlantic	3550	^{14}C-glutamate	272 nM	130 days	total substrate uptake	380 ng $l^{-1}d^{-1}$	1 ng $l^{-1}d^{-1}$	NI	38	Tabor et al. (1981)	
Cape Basin	5220	^{14}C-acetate	56.1 nM	17 days	total substrate uptake	15 ng $l^{-1}d^{-1}$	ND	NI	ND	Tabor et al. (1981)	
Cape Basin	5225	^{14}C-glutamate	211 nM	21 days	total substrate uptake	10 ng $l^{-1}d^{-1}$	ND	NI	ND	Tabor et al. (1981)	
Angola Basin	5220	^{14}C-glutamate	143 nM	40 days	total substrate uptake	71 ng $l^{-1}d^{-1}$	ND	NI	ND	Tabor et al. (1981)	
Angola Basin	5200	^{14}C-glutamate	653 nM	27 days	total substrate uptake	11 ng $l^{-1}d^{-1}$	ND	NI	ND	Tabor et al. (1981)	
NW Atlantic	1830	^{14}C-glutamate	3.40 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.37	Jannasch & Wirsen (1982)	(f)
NW Atlantic	3060	^{14}C-glutamate	4.18 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.31	Jannasch & Wirsen (1982)	(f)
Bermuda area	1800	^{14}C-glutamate	37.9 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.19	Jannasch & Wirsen (1982)	(f)
Bermuda area	3000	^{14}C-glutamate	39.3 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.5	Jannasch & Wirsen (1982)	(f)
N.W Atlantic	1830	^{14}C-casamino acids	0.426 mg l^{-1}	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.41	Jannasch & Wirsen (1982)	(f)
NW Atlantic	3500	^{14}C-casamino acids	0.286 mg l^{-1}	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.48	Jannasch & Wirsen (1982)	(f)
NW Atlantic	3130	^{14}C-casamino acids	1.40 mg l^{-1}	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.41	Jannasch & Wirsen (1982)	(f)
N.W Atlantic	1830	^{14}C-glucose	1.94 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.96	Jannasch & Wirsen (1982)	(f)
Puerto Rico	6000	^{14}C-glucose	1.05 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.45	Jannasch & Wirsen (1982)	(f)
Bermuda	1850	^{14}C-glucose	33.8 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.75	Jannasch & Wirsen (1982)	(f)
Bermuda	4500	^{14}C-glucose	30.3 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	2.65	Jannasch & Wirsen (1982)	(f)
Bermuda	4500	^{14}C-glucose	30.3 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	1.85	Jannasch & Wirsen (1982)	(f)
NW Atlantic	1770	^{14}C-acetate	8.2 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.59	Jannasch & Wirsen (1982)	(f)
NW Atlantic	3850	^{14}C-acetate	7.7 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.99	Jannasch & Wirsen (1982)	(f)
NW Atlantic	1750	^{14}C-acetate	99.3 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	1	Jannasch & Wirsen (1982)	(f)
NW Atlantic	4620	^{14}C-acetate	72.0 µM	3 weeks	total substrate utilization	ND (e)	ND (e)	NI	0.69	Jannasch & Wirsen (1982)	(f)

Bay of Biscay (NW Atlantic)	4700	^{14}C-glutamate	13 nM	2 hours	total substrate uptake	19.2 ng g^{-1} d^{-1}	6.43 ng g^{-1} d^{-1}	sediments	2.99	Rowe & Deming (1985)	(REC)
Bay of Biscay (NW Atlantic)	4700	^{14}C-glutamate	Concentration kinetic	2 hours	total substrate uptake	108.0 ng g^{-1} d^{-1}	44.5 ng g^{-1} d^{-1}	sediments	2.42	Rowe & Deming (1985)	(REC)
Demerara abyssal plain (N Atlantic)	4470	^{14}C-glutamate	63.9 nM	3 days	total substrate utilization	1.31 ± 0.12 dpm l^{-1} h^{-1}	0.75 ± 0.12 dpm l^{-1} h^{-1}	sediments (0–1 cm)	1.74	Deming & Colwell (1985)	(REC)
Demerara abyssal plain (N Atlantic)	4470	^{14}C-glutamate	63.9 nM	3 days	total substrate utilization	1.49 ± 0.19 dpm l^{-1} h^{-1}	0.58 ± 0.17 dpm l^{-1} h^{-1}	sediments (4–5 cm)	2.57	Deming & Colwell (1985)	(REC)
Demerara abyssal plain (N Atlantic)	4850	^{14}C-glutamate	63.9 nM	3 days	total substrate utilization	2.40 ± 0.72 dpm l^{-1} h^{-1}	0.79 ± 0.19 dpm l^{-1} h^{-1}	sediments (0–1 cm)	3.03	Deming & Colwell (1985)	(REC)
Demerara abyssal plain (N Atlantic)	4850	^{14}C-glutamate	63.9 nM	3 days	total substrate utilization	1.19 ± 0.19 dpm l^{-1} h^{-1}	0.82 ± 0.16 dpm l^{-1} h^{-1}	sediments (4–5 cm)	1.46	Deming & Colwell (1985)	(REC)
Demerara abyssal plain (N Atlantic)	4850	^{14}C-glutamate	63.9 nM	3 days	total substrate utilization	0.52 ± 0.16 dpm l^{-1} h^{-1}	0.15 ± 0.12 dpm l^{-1} h^{-1}	sediments (14-15 cm)	3.5	Deming & Colwell (1985)	(REC)
Mediterranean (Gulf of Marseille)	1100	^{14}C-glucose	5.8 nM	3 hours	substrate incorporation	78.5 ± 24 pg C l^{-1} h^{-1}	30.7 ± 10 pg C l-1 h-1	stratified	2.55	Bianchi & Garcin (1994)	(g)
Mediterranean (Ligurian Sea)	1100	^{14}C-glucose	5.8 nM	3 hours	substrate incorporation	59.5 ± 11 pg C l-1 h-1	23.6 ± 14 pg C l-1 h-1	stratified	2.52	Bianchi & Garcin (1994)	(h)
Mediterranean (Ligurian Sea)	1100	^{14}C-glucose	5.8 nM	3 hours	substrate incorporation	14.5 ± 6 pg C l-1 h-1	421.2 ± 43 pg C l-1 h-1	mixed	0.03	Bianchi & Garcin (1994)	(h)
NE Atlantic	4416	^{3}H-thymidine	5 nM	24 hours	production	16.0 ± 6.8 fmol l^{-1} h^{-1}	0.26 ± 1.2 fmol l^{-1} h^{-1}	NI - stratified	61.54	Poremba (1994)	(REC)
NE Atlantic	1812	^{3}H-thymidine	5 nM	24 hours	production	8.8 ± 5.1 fmol l^{-1} h^{-1}	3.4 ± 3.4 fmol l^{-1} h^{-1}	NI - stratified	2.59	Poremba (1994)	(REC)
NE Atlantic	3657	^{3}H-thymidine	5 nM	24 hours	production	9.6 ± 4.6 fmol l^{-1} h^{-1}	7.4 ± 5.6 fmol l^{-1} h^{-1}	NI - stratified	1.27	Poremba (1994)	(REC)
NE Atlantic	3019	^{3}H-leucine	10 nM	24 hours	production	672 ± 173 fmol l^{-1} h^{-1}	577 ± 112 fmol l^{-1} h^{-1}	NI - stratified	1.16	Poremba (1994)	(REC)
NE Atlantic	4416	^{3}H-leucine	10 nM	24 hours	production	339 ± 115 fmol l^{-1} h^{-1}	368 ± 133 fmol l^{-1} h^{-1}	NI - stratified	1.09	Poremba (1994)	(REC)
NE Atlantic	1812	^{3}H-leucine	10 nM	24 hours	production	128 ± 36 fmol l^{-1} h^{-1}	133 ± 91 fmol l^{-1} h^{-1}	NI - stratified	0.96	Poremba (1994)	(REC)
NE Atlantic (PAP site)	4800	^{3}H-thymidine	5 nM	24 hours	production	1.75 ± 0.43 fmol l^{-1} h^{-1}	2.62 ± 0.42 fmol l^{-1} h^{-1}	near bottom water	0.67	Patching & Eardly (1997)	(REC)
NE Atlantic (PAP site)	4800	^{3}H-thymidine	5 nM	24 hours	production	58.83 ± 2.36 fmol l^{-1} h^{-1}	21.33 ± 1.72 fmol l^{-1} h^{-1}	sediment contact water	2.76	Patching & Eardly (1997)	(REC)
NE Atlantic (PAP site)	4800	^{3}H-thymidine	5 nM	24 hours	production	31.19 ± 2.32 fmol l^{-1} h^{-1}	17.02 ± 1.32 fmol l^{-1} h^{-1}	sediment contact water	1.83	Patching & Eardly (1997)	(REC)
NE Atlantic (PAP site)	4800	^{3}H-thymidine	5 nM	24 hours	production	7.10 ± 0.78 fmol l^{-1} h^{-1}	4.14 ± 0.47 fmol l^{-1} h^{-1}	sediment contact water	1.71	Patching & Eardly (1997)	(REC)
NE Atlantic (PAP site)	4500	^{3}H-thymidine	5 nM	24 hours	production	0.24 ± 0.17 fmol l^{-1} h^{-1}	0.22 ± 0.13 fmol l^{-1} h^{-1}	near bottom water	1.09	Patching & Eardly (1997)	(REC)
NE Atlantic (PAP site)	4500	^{3}H-thymidine	5 nM	24 hours	production	2.39 ± 0.26 fmol l^{-1} h^{-1}	0.70 ± 0.15 fmol l^{-1} h^{-1}	sediment contact water	3.41	Patching & Eardly (1997)	(REC)
NE Atlantic (PAP site)	4500	^{3}H-thymidine	5 nM	24 hours	production	5.42 ± 0.93 fmol l^{-1} h^{-1}	0.71 ± 0.24 fmol l^{-1} h^{-1}	sediment contact water	7.63	Patching & Eardly (1997)	(REC)
NE Atlantic (PAP site)	4500	^{3}H-leucine	5 nM	24 hours	production	0.89 ± 0.57 fmol l^{-1} h^{-1}	0.14 ± 1.94 fmol l^{-1} h^{-1}	sediment contact water	1.00	Patching & Eardly (1997)	(REC)
NE Atlantic (PAP site)	4500	^{3}H-leucine	5 nM	24 hours	production	13.22 ± 3.14 fmol l^{-1} h^{-1}	2.03 ± 1.69 fmol l^{-1} h^{-1}	sediment contact water	6.51	Patching & Eardly (1997)	(REC)
Mediterranean (Ligurian Sea)	1150	^{14}C-amino acids	10 nM	12 hours	total substrate uptake	48.9 ± 7.8 pM C h^{-1}	22.7 ± 1.8 pM C h^{-1}	stratified	2.2	Bianchi et al. (1999b)	(i)
Mediterranean (Ligurian Sea)	1150	^{14}C-amino acids	10 nM	12 hours	total substrate uptake	209.2 ± 7.1 pM C h^{-1}	212.2 ± 5.4 pM C h^{-1}	fecal pellets	0.9	Bianchi et al. (1999b)	(i)
Mediterranean (Ligurian Sea)	1150	^{14}C-amino acids	10 nM	12 hours	total substrate uptake	209.8 ± 10 pM C h^{-1}	222.6 ± 13 pM C h^{-1}	fecal pellets	0.9	Bianchi et al. (1999b)	(i)
Mediterranean (Ligurian Sea)	1150	^{3}H-thymidine	5 nM	12 hours	production	7.83 ± 0.4 pM C h^{-1}	5.0 ± 1.0 pM C h^{-1}	stratified	1.6	Bianchi et al. (1999b)	(i)
Mediterranean (Ligurian Sea)	1150	^{3}H-thymidine	5 nM	12 hours	production	7.06 ± 0.8 pM C h^{-1}	4.6 ± 0.7 pM C h^{-1}	stratified	1.5	Bianchi et al. (1999b)	(i)
Mediterranean (Ligurian Sea)	1150	^{3}H-thymidine	5 nM	12 hours	production	107.5 ± 4.0 pM C h^{-1}	120.2 ± 2.1 pM C h^{-1}	fecal pellets	0.9	Bianchi et al. (1999b)	(i)
Mediterranean (Ligurian Sea)	1150	^{3}H-thymidine	5 nM	12 hours	production	196.0 ± 6.0 pM C h^{-1}	169.6 ± 8.2 pM C h^{-1}	fecal pellets	1.1	Bianchi et al. (1999b)	(i)
Mediterranean (Marseille)	800	^{14}C-glucose	10 nM	12 hours	total substrate uptake	58.4 ± 3.2 pM C h^{-1}	5.2 ± 0.5 pM C h^{-1}	stratified	11.2	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	800	^{14}C-amino acids	10 nM	12 hours	total substrate uptake	209.8 ± 10.6 pM C h^{-1}	222.6 ± 6 pM C h^{-1}	stratified	0.94	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	800	^{14}C-glucose	10 nM	12 hours	total substrate uptake	31.4 ± 2.6 pM C h^{-1}	5.7 ± 1.1 pM C h^{-1}	stratified	5.5	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1000	^{14}C-glucose	10 nM	12 hours	total substrate uptake	15.9 ± 4.5 pM C h^{-1}	16.0 ± 2.0 pM C h^{-1}	stratified	0.99	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1000	^{14}C-glucose	10 nM	12 hours	total substrate uptake	63.5 ± 2.7 pM C h^{-1}	51.0 ± 8.7 pM C h^{-1}	stratified	1.25	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1000	^{14}C-glucose	10 nM	12 hours	total substrate uptake	8.0 ± 2.1 pM C h^{-1}	5.4 ± 1.1 pM C h^{-1}	stratified	1.48	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1000	^{14}C-glucose	10 nM	12 hours	total substrate uptake	12.3 ± 5.4 pM C h^{-1}	8.0 ± 1.8 pM C h^{-1}	stratified	1.53	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1000	^{14}C-glucose	10 nM	12 hours	total substrate uptake	2.2 ± 0.6 pM C h^{-1}	1.1 ± 0.1 pM C h^{-1}	stratified	2	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1150	^{14}C-glucose	10 nM	12 hours	total substrate uptake	7.1 ± 0.4 pM C h^{-1}	3.6 ± 0.2 pM C h^{-1}	stratified	1.97	Tholosan et al. (1999)	
Mediterranean (Marseille)	1150	^{14}C-glucose	10 nM	12 hours	total substrate uptake	209.2 ± 7.1 pM C h^{-1}	212.2 ± 5.4 pM C h^{-1}	stratified	0.99	Tholosan et al. (1999)	
Mediterranean (Marseille)	1150	^{14}C-glucose	10 nM	12 hours	total substrate uptake	48.9 ± 7.8 pM C h^{-1}	22.7 ± 1.8 pM C h^{-1}	stratified	2.15	Tholosan et al. (1999)	
Mediterranean (Marseille)	1150	^{14}C-glucose	10 nM	12 hours	total substrate uptake	78.2 ± 13.6 pM C h^{-1}	15.1 ± 3.2 pM C h^{-1}	stratified	5.2	Tholosan et al. (1999)	
Mediterranean (Marseille)	1150	^{14}C-glucose	10 nM	12 hours	total substrate uptake	35.4 ± 2.7 pM C h^{-1}	4.4 ± 0.8 pM C h^{-1}	stratified	8	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1500	^{14}C-glucose	10 nM	12 hours	total substrate uptake	8.4 ± 0.5 pM C h^{-1}	4.8 ± 0.6 pM C h^{-1}	stratified	1.75	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1500	^{14}C-glucose	10 nM	12 hours	total substrate uptake	33.9 ± 2.1 pM C h^{-1}	18.9 ± 0.3 pM C h^{-1}	stratified	1.8	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1500	^{14}C-glucose	10 nM	12 hours	total substrate uptake	25.0 ± 2.3 pM C h^{-1}	19.9 ± 0.8 pM C h^{-1}	stratified	1.25	Tholosan et al. (1999)	

Mediterranean (Ligurian Sea)	1500	^{14}C-glucose	10 nM	12 hours	total substrate uptake	9.6 ± 1.5 pM C h^{-1}	4.6 ± 0.1 pM C h^{-1}	stratified	2.08	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1500	^{14}C-amino acids	10 nM	12 hours	total substrate uptake	294.6 ± 22.0 pM C h^{-1}	142.3 ± 11.9 pM C h^{-1}	stratified	2.07	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	2000	^{14}C-glucose	10 nM	12 hours	total substrate uptake	6.6 ± 0.6 pM C h^{-1}	3.4 ± 0.5 pM C h^{-1}	stratified	1.94	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	2000	^{14}C-glucose	10 nM	12 hours	total substrate uptake	37.9 ± 4.5 pM C h^{-1}	37.9 ± 4.3 pM C h^{-1}	stratified	1	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	2000	^{14}C-glucose	10 nM	12 hours	total substrate uptake	10.0 ± 0.7 pM C h^{-1}	6.6 ± 0.5 pM C h^{-1}	stratified	1.51	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	2000	^{14}C-glucose	10 nM	12 hours	total substrate uptake	22.2 ± 1.4 pM C h^{-1}	0.79 ± 1.4 pM C h-1	stratified	28.1	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	2000	^{14}C-amino acids	10 nM	12 hours	total substrate uptake	156.0 ± 2.6 pM C h^{-1}	120.2 ± 2.6 pM C h^{-1}	stratified	1.29	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	2000	^{14}C-glucose	10 nM	12 hours	total substrate uptake	1.8 ± 0.2 pM C h^{-1}	0.72 ± 0.1 pM C h^{-1}	stratified	2.5	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	800	^{3}H-thymidine	5 nM	12 hours	production	196.1 pM C h^{-1}	166.9 pM C h^{-1}	stratified	1.17	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	800	^{3}H-thymidine	5 nM	12 hours	production	479.2 pM C h^{-1}	173.0 pM C h^{-1}	stratified	2.76	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1000	^{3}H-thymidine	5 nM	12 hours	production	113.2 pM C h^{-1}	8.8 pM C h^{-1}	stratified	12.9	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1000	^{3}H-thymidine	5 nM	12 hours	production	53.3 pM C h^{-1}	35.8 pM C h^{-1}	stratified	1.49	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1000	^{3}H-thymidine	5 nM	12 hours	production	19.6 pM C h^{-1}	9.3 pM C h^{-1}	stratified	2.12	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1000	^{3}H-thymidine	5 nM	12 hours	production	73.6 pM C h^{-1}	60.6 pM C h^{-1}	stratified	1.22	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1150	^{3}H-thymidine	5 nM	12 hours	production	7.8 pM C h^{-1}	5.0 pM C h^{-1}	stratified	1.57	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1150	^{3}H-thymidine	5 nM	12 hours	production	7.1 pM C h^{-1}	4.6 pM C h^{-1}	stratified	1.56	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1150	^{3}H-thymidine	5 nM	12 hours	production	107.5 pM C h^{-1}	120.3 pM C h^{-1}	stratified	0.89	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1500	^{3}H-thymidine	5 nM	12 hours	production	50.0 pM C h^{-1}	22.1 pM C h^{-1}	stratified	2.26	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1500	^{3}H-thymidine	5 nM	12 hours	production	35.4 pM C h^{-1}	15.4 pM C h^{-1}	stratified	2.3	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	1500	^{3}H-thymidine	5 nM	12 hours	production	102.8 pM C h^{-1}	65.8 pM C h^{-1}	stratified	1.56	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	2000	^{3}H-thymidine	5 nM	12 hours	production	3.3 pM C h^{-1}	1.9 pM C h^{-1}	stratified	1.74	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	2000	^{3}H-thymidine	5 nM	12 hours	production	88.1 pM C h^{-1}	54.6 pM C h^{-1}	stratified	1.61	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	2000	^{3}H-thymidine	5 nM	12 hours	production	18.8 pM C h^{-1}	1.1 pM C h^{-1}	stratified	17.08	Tholosan et al. (1999)	
Mediterranean (Ligurian Sea)	800	^{3}H-thymidine	5 nM	12 hours	production	197.5 pM C h^{-1}	162.5 pM C h^{-1}	stratified	1.22	Tholosan (1999)	
Mediterranean (Ligurian Sea)	1000	^{3}H-thymidine	5 nM	12 hours	production	186.4 pM C h^{-1}	86.8 pM C h^{-1}	stratified	2.15	Tholosan (1999)	
Mediterranean (Ligurian Sea)	1500	^{3}H-thymidine	5 nM	12 hours	production	100.8 pM C h^{-1}	37.3 pM C h^{-1}	stratified	2.7	Tholosan (1999)	
Mediterranean (Ligurian Sea)	1500	^{3}H-thymidine	5 nM	12 hours	production	73.8 pM C h^{-1}	28.9 pM C h^{-1}	stratified	2.55	Tholosan (1999)	
Mediterranean (Ligurian Sea)	2000	^{3}H-thymidine	5 nM	12 hours	production	188.6 pM C h^{-1}	98.5 pM C h^{-1}	stratified	1.91	Tholosan (1999)	
Mediterranean (Ligurian Sea)	2000	^{3}H-thymidine	5 nM	12 hours	production	87.5 pM C h^{-1}	35.8 pM C h^{-1}	stratified	2.44	Tholosan (1999)	
Mediterranean (Ligurian Sea)	2000	^{3}H-thymidine	5 nM	12 hours	production	45.6 pM C h^{-1}	10.8 pM C h^{-1}	stratified	4.22	Tholosan (1999)	
Mediterranean (Ligurian Sea)	850	^{3}H-leucine	5 nM	12 hours	production	2.37 ng C l-1h-1	2.00 ng C l-1h-1	stratified	1.19	Bianchi et al. (1999a)	
Mediterranean (Ligurian Sea)	1300	^{3}H-leucine	5 nM	12 hours	production	1.31 ng C l-1h-1	0.79 ng C l-1h-1	stratified	1.66	Bianchi et al. (1999a)	
Mediterranean (Ligurian Sea)	1500	^{3}H-leucine	5 nM	12 hours	production	1.20 ng C l-1h-1	0.54 ng C l-1h-1	stratified	2.22	Bianchi et al. (1999a)	
Mediterranean (Ligurian Sea)	2000	^{3}H-leucine	5 nM	12 hours	production	1.05 ng C l-1h-1	0.48 ng C l-1h-1	stratified	2.19	Bianchi et al. (1999a)	
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	0.012 ± 0.001 fmol cm^{-3} h^{-1}	ND	sediment contact water	2.1	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	23.6 ± 15.1 fmol cm^{-3} h^{-1}	ND	sediments (0–1 cm)	1.8	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	17.3 ± 10.7 fmol cm^{-3} h^{-1}	ND	sediments (1-2 cm)	3.2	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	15.9 ± 10.4 fmol cm^{-3} h^{-1}	ND	sediments (2-3 cm)	1.9	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	22.9 ± 23.7 fmol cm^{-3} h^{-1}	ND	sediments (3-4 cm)	2.3	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	11.1 ± 13.4 fmol cm^{-3} h^{-1}	ND	sediments (4-5 cm)	0.7	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	0.005 ± 0.001 fmol cm^{-3} h^{-1}	ND	sediment contact water	0.1	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	14.5 ± 2.4 fmol cm^{-3} h^{-1}	ND	sediments (0–1 cm)	1.6	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	7.3 ± 3.1 fmol cm^{-3} h^{-1}	ND	sediments (1-2 cm)	1.4	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	7.3 ± 3.4 fmol cm^{-3} h^{-1}	ND	sediments (2-3 cm)	1.2	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	10.9 ± 6.1 fmol cm^{-3} h^{-1}	ND	sediments (3-4 cm)	1.5	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	8.0 ± 4.6 fmol cm^{-3} h^{-1}	ND	sediments (4-5 cm)	1.5	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	0.005 ± 0.002 fmol cm^{-3} h^{-1}	ND	sediment contact water	1.8	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	14.2 ± 2.3 fmol cm^{-3} h^{-1}	ND	sediments (0–1 cm)	1.5	Eardly et al. (2011)	(REC)

NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	9.2 ± 3.5 fmol cm^{-3} h^{-1}	ND	sediments (1-2 cm)	1.3	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	6.2 ± 2.9 fmol cm^{-3} h^{-1}	ND	sediments (2-3 cm)	1.2	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	5.1 ± 2.7 fmol cm^{-3} h^{-1}	ND	sediments (3-4 cm)	0.7	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	4.2 ± 2.0 fmol cm^{-3} h^{-1}	ND	sediments (4-5 cm)	0.7	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	0.01 ± 0.007 fmol cm^{-3} h^{-1}	ND	sediment contact water	0.7	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	8.5 ± 1.9 fmol cm^{-3} h^{-1}	ND	sediments (0–1 cm)	1.1	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	6.0 ± 1.9 fmol cm^{-3} h^{-1}	ND	sediments (1-2 cm)	0.9	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	4.5 ± 1.3 fmol cm^{-3} h^{-1}	ND	sediments (2-3 cm)	1	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	9.9 ± 5.4 fmol cm^{-3} h^{-1}	ND	sediments (3-4 cm)	1.1	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-thymidine	24 nM	24 hours	production	4.5 ± 0.4 fmol cm^{-3} h^{-1}	ND	sediments (4-5 cm)	0.9	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	51.9 ± 38.5 fmol cm^{-3} h^{-1}	ND	sediments (0–1 cm)	1.4	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	103.5 ± 77.3 fmol cm^{-3} h^{-1}	ND	sediments (1-2 cm)	1.3	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	109.0 ± 12.1 fmol cm^{-3} h^{-1}	ND	sediments (2-3 cm)	1.5	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	149.3 ± 58.7 fmol cm^{-3} h^{-1}	ND	sediments (3-4 cm)	1.6	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	14.4 ± 3.9 fmol cm^{-3} h^{-1}	ND	sediments (4-5 cm)	1.3	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	127.6 ± 59.2 fmol cm^{-3} h^{-1}	ND	sediments (0–1 cm)	2	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	61.6 ± 35.5 fmol cm^{-3} h^{-1}	ND	sediments (1-2 cm)	2	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	22.9 ± 3.6 fmol cm^{-3} h^{-1}	ND	sediments (2-3 cm)	0.8	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	51.1 ± 26 fmol cm^{-3} h^{-1}	ND	sediments (3-4 cm)	1.4	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	67.7 ± 49.1 fmol cm^{-3} h^{-1}	ND	sediments (4-5 cm)	2.5	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	161.4 ± 78.4 fmol cm^{-3} h^{-1}	ND	sediments (0–1 cm)	2.1	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	66.2 ± 37.7 fmol cm^{-3} h^{-1}	ND	sediments (1-2 cm)	2.1	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	50.2 ± 12.7 fmol cm^{-3} h^{-1}	ND	sediments (2-3 cm)	2.9	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	91.7 ± 21.2 fmol cm^{-3} h^{-1}	ND	sediments (3-4 cm)	3.5	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	98.7 ± 21.5 fmol cm^{-3} h^{-1}	ND	sediments (4-5 cm)	2	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	105.3 ± 8.7 fmol cm^{-3} h^{-1}	ND	sediments (0–1 cm)	1.2	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	91.1 ± 26.7 fmol cm^{-3} h^{-1}	ND	sediments (1-2 cm)	1.4	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	144.8 ± 100.7 fmol cm^{-3} h^{-1}	ND	sediments (2-3 cm)	1.3	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	144.7 ± 137.9 fmol cm^{-3} h^{-1}	ND	sediments (3-4 cm)	1.5	Eardly et al. (2011)	(REC)
NE Atlantic (PAP site)	4850	^{3}H-leucine	11 nM	24 hours	production	53.1 ± 13.6 fmol cm^{-3} h^{-1}	ND	sediments (4-5 cm)	1.5	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-thymidine	24 nM	24 hours	production	0.004 ± 0.002 fmol cm^{-3} h^{-1}	ND	sediment contact water	5.5	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-thymidine	24 nM	24 hours	production	1.7 ± 0.1 fmol cm^{-3} h^{-1}	ND	sediments (0–2 cm)	1	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-thymidine	24 nM	24 hours	production	0.8 ± 0.9 fmol cm^{-3} h^{-1}	ND	sediments (3–5 cm)	0.6	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-leucine	11 nM	24 hours	production	11.7 ± 5.3 fmol cm^{-3} h^{-1}	ND	sediments (0–2 cm)	1.4	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-leucine	11 nM	24 hours	production	4.1 ± 1.6 fmol cm^{-3} h^{-1}	ND	sediments (3–5 cm)	0.6	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-leucine	11 nM	24 hours	production	3.3 ± 3.5 fmol cm^{-3} h^{-1}	ND	sediments (5–10 cm)	1.5	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-thymidine	24 nM	24 hours	production	0.007 ± 0.0008 fmol cm^{-3} h^{-1}	ND	sediment contact water	1.7	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-thymidine	24 nM	24 hours	production	4.2 ± 1.6 fmol cm^{-3} h^{-1}	ND	sediments (0–2 cm)	3.4	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-thymidine	24 nM	24 hours	production	4.6 ± 1.5 fmol cm^{-3} h^{-1}	ND	sediments (3–5 cm)	6.9	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-thymidine	24 nM	24 hours	production	4.7 ± 4.7 fmol cm^{-3} h^{-1}	ND	sediments (5–10 cm)	2.4	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-leucine	11 nM	24 hours	production	5.9 ± 2.7 fmol cm^{-3} h^{-1}	ND	sediments (0–2 cm)	1.3	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-leucine	11 nM	24 hours	production	4.1 ± 1.0 fmol cm^{-3} h^{-1}	ND	sediments (3–5 cm)	1.9	Eardly et al. (2011)	(REC)
NE Atlantic (Eumeli-site)	4550	^{3}H-leucine	11 nM	24 hours	production	3.4 ± 2.1 fmol cm^{-3} h^{-1}	ND	sediments (5–10 cm)	1.9	Eardly et al. (2011)	(REC)
Mediterranean (Ligurian Sea)	1000	^{3}H-leucine	10 nM	12 hours	production	0.77 ± 0.10 ng C l^{-1} h^{-1}	0.48 ± 0.15 ng C l^{-1} h^{-1}	stratified	1.6	Tamburini et al. (2002)	
Mediterranean (Ligurian Sea)	1500	^{3}H-leucine	10 nM	12 hours	production	0.74 ± 0.39 ng C l^{-1} h^{-1}	0.28 ± 0.12 ng C l^{-1} h^{-1}	stratified	2.6	Tamburini et al. (2002)	
Mediterranean (Ligurian Sea)	2000	^{3}H-leucine	10 nM	12 hours	production	0.47 ± 0.11 ng C l^{-1} h^{-1}	0.21 ± 0.11 ng C l^{-1} h^{-1}	stratified	2.2	Tamburini et al. (2002)	
Mediterranean (Ligurian Sea)	2000	^{3}H-leucine	10 nM	12 hours	production	2.06 ± 0.06 ng C l^{-1} h^{-1}	0.13 ± 0.14 ng C l^{-1} h^{-1}	stratified	15.8	Tamburini et al. (2002)	
Mediterranean (Ligurian Sea)	1500	MUF-phosphate	0.05 µM	12 hours	phosphatase (H_i; % ± SE)	7.2 ± 1.9	3.1 % ± 0.7	stratified	2.32	Tamburini et al. (2002)	

Table S2. Pressure effect on microbial activity measurements for shallow-water samples incubated under both atmospheric and higher pressures, compiled from the literature.

Sampling area	Free-living (f) or attached prokaryotes (a)	Sampling detph (m)	with or without particles	Added substrate	Metabolic process	Higher pressure tested (MPa)	Pressure effect	Reference
NE Atlantic Ocean	f	10	without	^{3}H-leucine	production	10	0.5	Turley (1993)
NE Atlantic Ocean	f	10	without	^{3}H-leucine	production	20	0.25	Turley (1993)
NE Atlantic Ocean	f	10	without	^{3}H-leucine	production	30	0.15	Turley (1993)
NE Atlantic Ocean	f	10	without	^{3}H-leucine	production	43	0.22	Turley (1993)
NE Atlantic Ocean	f	10	without	^{3}H-thymidine	production	10	0.21	Turley (1993)
NE Atlantic Ocean	f	10	without	^{3}H-thymidine	production	20	0.12	Turley (1993)
NE Atlantic Ocean	f	10	without	^{3}H-thymidine	production	30	0.08	Turley (1993)
NE Atlantic Ocean	f	10	without	^{3}H-thymidine	production	43	0.11	Turley (1993)
NE Atlantic Ocean	f	40	without	^{3}H-leucine	production	10	0.62	Turley (1993)
NE Atlantic Ocean	f	40	without	^{3}H-leucine	production	20	0.27	Turley (1993)
NE Atlantic Ocean	f	40	without	^{3}H-leucine	production	30	0.12	Turley (1993)
NE Atlantic Ocean	f	40	without	^{3}H-leucine	production	43	0.05	Turley (1993)
NE Atlantic Ocean	a	200	with	^{3}H-leucine	production	10	1.04	Turley (1993)
NE Atlantic Ocean	a	200	with	^{3}H-leucine	production	20	0.37	Turley (1993)
NE Atlantic Ocean	a	200	with	^{3}H-leucine	production	30	0.25	Turley (1993)
NE Atlantic Ocean	a	200	with	^{3}H-leucine	production	43	0.18	Turley (1993)
NE Atlantic Ocean	a	200	with	^{3}H-thymidine	production	10	0.78	Turley (1993)
NE Atlantic Ocean	a	200	with	^{3}H-thymidine	production	20	0.56	Turley (1993)
NE Atlantic Ocean	a	200	with	^{3}H-thymidine	production	30	0.15	Turley (1993)
NE Atlantic Ocean	a	200	with	^{3}H-thymidine	production	43	0.01	Turley (1993)
NW Mediterranean Sea	f	200	with fresh diatom detritus	MCA-Leu	aminopeptidase	8	0.30	Tamburini et al. (2006)
NW Mediterranean Sea	f	200	with fresh diatom detritus	MCA-Leu	aminopeptidase	14	0.56	Tamburini et al. (2006)
NW Mediterranean Sea	f	200	with fresh diatom detritus	MCA-Leu	aminopeptidase	5	0.10	Tamburini et al. (2006)
NW Mediterranean Sea	f	200	with fresh diatom detritus	MCA-Leu	aminopeptidase	8	0.45	Tamburini et al. (2006)
NW Mediterranean Sea	f	200	with fresh diatom detritus	MCA-Leu	aminopeptidase	11	0.40	Tamburini et al. (2006)
NW Mediterranean Sea	f	200	with fresh diatom detritus	MCA-Leu	aminopeptidase	14	0.27	Tamburini et al. (2006)
NW Mediterranean Sea	f	200	without	MCA-Leu	aminopeptidase	5	0.20	Tamburini et al. (2006)
NW Mediterranean Sea	f	200	without	MCA-Leu	aminopeptidase	8	0.12	Tamburini et al. (2006)
NW Mediterranean Sea	f	200	without	MCA-Leu	aminopeptidase	11	0.14	Tamburini et al. (2006)
NW Mediterranean Sea	f	200	without	MCA-Leu	aminopeptidase	14	0.20	Tamburini et al. (2006)

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Mediterranean (Ligurian Sea)	2000	MUF-phosphate	5 µM	12 hours	phosphatase (V_{max} ± SE)	468 ± 203 pM MUF h^{-1}	335 ± 40 pM MUF h^{-1}	stratified	1.4	Tamburini et al. (2002)	
Mediterranean (Ligurian Sea)	2000	MUF-phosphate	5 µM	12 hours	phosphatase (V_{max} ± SE)	443 ± 199 pM MUF h^{-1}	168 ± 70 pM MUF h^{-1}	stratified	2.64	Tamburini et al. (2002)	
Mediterranean (Ligurian Sea)	1000	MCA-leu	0.05 µM	12 hours	aminopeptidase (H_i; % ± SE)	11.0 ± 4.4	3.9 % ± 2.4	stratified	2.82	Tamburini et al. (2002)	
Mediterranean (Ligurian Sea)	2000	MCA-leu	5 µM	12 hours	aminopeptidase (V_{max} ± SE)	835 ± 99 pM MCA h^{-1}	571 ± 68 pM MCA h^{-1}	stratified	1.46	Tamburini et al. (2002)	
Mediterranean (Ligurian Sea)	2000	MCA-leu	5 µM	12 hours	aminopeptidase (V_{max} ± SE)	386 ± 20 pM MCA h^{-1}	137 ± 96 pM MCA h^{-1}	stratified	2.82	Tamburini et al. (2002)	
Mediterranean (Ionian Sea)	2500	^{3}H-leucine	10 nM	10 hours	production	1.5 ng C l^{-1} h^{-1}	0.1 ng C l^{-1} h^{-1}	stratified	15	Tamburini (2002)	
Mediterranean (Ionian Sea)	3000	^{3}H-leucine	10 nM	10 hours	production	1.6 ng C l^{-1} h^{-1}	0.7 ng C l^{-1} h^{-1}	stratified	2.29	Tamburini (2002)	
Mediterranean (Ionian Sea)	1500	^{14}C-glutamate	10 nM	12 hours	substrate incorporation	1.2 nM h^{-1}	0.7 nM h^{-1}	stratified	1.71	Tamburini (2002)	
Mediterranean (Ionian Sea)	1500	^{14}C-glutamate	10 nM	12 hours	substrate respiration	2.7 nM h^{-1}	1.7 nM h^{-1}	stratified	1.59	Tamburini (2002)	
Mediterranean (Ionian Sea)	2500	^{14}C-glutamate	10 nM	12 hours	substrate incorporation	4.0 nM h^{-1}	0.9 nM h^{-1}	stratified	4.44	Tamburini (2002)	
Mediterranean (Ionian Sea)	2500	^{14}C-glutamate	10 nM	12 hours	substrate respiration	29.8 nM h^{-1}	7.9 nM h^{-1}	stratified	3.77	Tamburini (2002)	
Mediterranean (Ionian Sea)	2500	^{14}C-glutamate	10 nM	12 hours	substrate incorporation	112.2 nM h^{-1}	20.6 nM h^{-1}	stratified	5.45	Tamburini (2002)	
Mediterranean (Ionian Sea)	3000	^{14}C-glutamate	10 nM	12 hours	substrate respiration	15.7 nM h^{-1}	2.3 nM h^{-1}	stratified	6.83	Tamburini (2002)	
Mediterranean anoxic brine (Bannock)	3300	^{14}C-glutamate	10 nM	12 hours	substrate incorporation	3.98 nM h^{-1}	0.07 nM h^{-1}	anoxic brine	56.86	Tamburini (2002)	
Mediterranean anoxic brine (Bannock)	3300	^{14}C-glutamate	10 nM	12 hours	substrate respiration	15.02 nM h^{-1}	3.42 nM h^{-1}	anoxic brine	4.39	Tamburini (2002)	
Mediterranean anoxic brine (Bannock)	3300	^{3}H-leucine	10 nM	10 hours	production	1.24 nM h^{-1}	0.36 nM h^{-1}	anoxic brine	3.44	Tamburini (2002)	
Mediterranean anoxic brine (L'Atalante)	3500	^{3}H-leucine	10 nM	10 hours	production	0.12 nM h^{-1}	0.07 nM h^{-1}	anoxic brine	1.71	Tamburini (2002)	
Mediterranean anoxic brine (Bannock)	3300	MCA-leu	5 µM	10 hours	aminopeptidase	0.44 nM h^{-1}	0.13 nM h^{-1}	anoxic brine	3.38	Tamburini (2002)	
Mediterranean anoxic brine (Bannock)	3300	MUF-P	5 µM	10 hours	phosphatase	2.28 nM h^{-1}	1.46 nM h^{-1}	anoxic brine	1.56	Tamburini (2002)	
NW Mediterranean Sea (Lacaze-Duthiers Canyon)	1000	^{14}C-glutamate	2 nM	4 hours	substrate incorporation	2.1 ± 1.0 pM h^{-1}	23.2 ± 1.0 pM h^{-1}	sediment contact water	0.09	Tamburini (2002)	
NW Mediterranean Sea (Lacaze-Duthiers Canyon)	1000	^{14}C-glutamate	2 nM	4 hours	substrate respiration	11.5 ± 2.2 pM h^{-1}	182.5 ± 9.5 pM h^{-1}	sediment contact water	0.06	Tamburini (2002)	
Mediterranean (Ligurian Sea)	1000	^{14}C-glutamate	10 nM	12 hours	substrate incorporation	1.67 ± 0.70 pM C h^{-1}	1.11 ± 0.89 pM C h^{-1}	stratified	1.50	Tamburini et al. (2003)	
Mediterranean (Ligurian Sea)	1000	^{14}C-glutamate	10 nM	12 hours	substrate respiration	6.20 ± 1.02 pM CO_2 h^{-1}	3.37 ± 0.21 pM CO_2 h^{-1}	stratified	1.84	Tamburini et al. (2003)	
Mediterranean (Ligurian Sea)	2000	^{14}C-glutamate	10 nM	12 hours	substrate incorporation	6.05 ± 0.04 pM C h^{-1}	1.25 ± 0.16 pM C h^{-1}	stratified	4.83	Tamburini et al. (2003)	
Mediterranean (Ligurian Sea)	2000	^{14}C-glutamate	10 nM	12 hours	substrate respiration	4.76 ± 1.21 pM CO_2 h^{-1}	2.47 ± 0.50 pM CO_2 h^{-1}	stratified	1.93	Tamburini et al. (2003)	
Mediterranean (Ligurian Sea)	1000	^{14}C-glutamate	10 nM	12 hours	substrate incorporation	4.76 ± 1.21 pM C h^{-1}	2.47 ± 0.50 pM C h^{-1}	stratified	2.41	Tamburini et al. (2003)	
Mediterranean (Ligurian Sea)	1000	^{14}C-glutamate	10 nM	12 hours	substrate respiration	22.10 ± 0.32 pM CO_2 h^{-1}	18.9 ± 0.75 pM CO_2 h^{-1}	stratified	1.17	Tamburini et al. (2003)	
Mediterranean (Ligurian Sea)	1500	^{14}C-glutamate	10 nM	12 hours	substrate incorporation	12.03 ± 3.63 pM C h^{-1}	0.78 ± 0.28 pM C h^{-1}	stratified	15.45	Tamburini et al. (2003)	
Mediterranean (Ligurian Sea)	1500	^{14}C-glutamate	10 nM	12 hours	substrate respiration	32.16 ± 1.03 pM CO_2 h^{-1}	2.52 ± 0.75 pM CO_2 h^{-1}	stratified	12.74	Tamburini et al. (2003)	
Mediterranean (Ligurian Sea)	2000	^{14}C-glutamate	10 nM	12 hours	substrate incorporation	1.52 ± 0.35 pM C h^{-1}	0.35 ± 0.05 pM C h^{-1}	stratified	4.32	Tamburini et al. (2003)	
Mediterranean (Ligurian Sea)	2000	^{14}C-glutamate	10 nM	12 hours	substrate respiration	1.15 ± 0.24 pM CO_2 h^{-1}	0.16 ± 0.01 pM CO_2 h^{-1}	stratified	6.98	Tamburini et al. (2003)	
Mediterranean (Ligurian Sea)	2000	^{14}C-glutamate	10 nM	12 hours	substrate incorporation	0.93 ± 0.12 pM C h^{-1}	0.50 ± 0.20 pM C h^{-1}	stratified	1.85	Tamburini et al. (2003)	
Gulf of Mexico	767	^{3}H-thymidine	10 µCi cm^{-3}	12 hours	production	4.6 µg m^{-2} d^{-1}	33 µg m^{-2} d^{-1}	sediments (0–1 cm)	0.14	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	987	^{3}H-thymidine	10 µCi cm^{-3}	12 hours	production	6.3 µg m^{-2} d^{-1}	35.7 µg m^{-2} d^{-1}	sediments (0–1 cm)	0.18	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	1828	^{3}H-thymidine	10 µCi cm^{-3}	12 hours	production	14.8 µg m^{-2} d^{-1}	33.6 µg m^{-2} d^{-1}	sediments (0–1 cm)	0.44	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	2700	^{3}H-thymidine	10 µCi cm^{-3}	12 hours	production	52.0 µg m^{-2} d^{-1}	26.6 µg m^{-2} d^{-1}	sediments (0–1 cm)	2.00	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	3470	^{3}H-thymidine	10 µCi cm^{-3}	12 hours	production	44.6 µg m^{-2} d^{-1}	19.5 µg m^{-2} d^{-1}	sediments (0–1 cm)	2.30	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	3535	^{3}H-thymidine	10 µCi cm^{-3}	12 hours	production	75.1 µg m^{-2} d^{-1}	109 µg m^{-2} d^{-1}	sediments (0–1 cm)	0.69	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	3535	^{14}C-amino acids	2.5 nCi cm^{-3}	12 hours	substrate respiration	0.097 nCi cm^{-3} h^{-1}	0.077 nCi cm^{-3} h^{-1}	sediments (0–1 cm)	1.28	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	3535	^{14}C-amino acids	2.5 nCi cm^{-3}	12 hours	substrate respiration	0.054 nCi cm^{-3} h^{-1}	0.057 nCi cm^{-3} h^{-1}	sediments (4-5 cm)	0.94	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	3535	^{14}C-amino acids	2.5 nCi cm^{-3}	12 hours	substrate respiration	0.049 nCi cm^{-3} h^{-1}	0.027 nCi cm^{-3} h^{-1}	sediments (9-10 cm)	1.82	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	3535	^{14}C-amino acids	2.5 nCi cm^{-3}	12 hours	substrate respiration	0.054 nCi cm^{-3} h^{-1}	0.048 nCi cm^{-3} h^{-1}	sediments (14-15 cm)	1.13	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	3470	^{14}C-amino acids	2.5 nCi cm^{-3}	12 hours	substrate respiration	0.021 nCi cm^{-3} h^{-1}	0.032 nCi cm^{-3} h^{-1}	sediments (0–1 cm)	0.66	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	3470	^{14}C-amino acids	2.5 nCi cm^{-3}	12 hours	substrate respiration	0.010 nCi cm^{-3} h^{-1}	0.033 nCi cm^{-3} h^{-1}	sediments (4-5 cm)	0.30	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	3470	^{14}C-amino acids	2.5 nCi cm^{-3}	12 hours	substrate respiration	0.026 nCi cm^{-3} h^{-1}	0.019 nCi cm^{-3} h^{-1}	sediments (9-10 cm)	1.38	Deming & Carpenter (2008)	(REC)
Gulf of Mexico	3470	^{14}C-amino acids	2.5 nCi cm^{-3}	12 hours	substrate respiration	0.019 nCi cm^{-3} h^{-1}	0.019 nCi cm^{-3} h^{-1}	sediments (14-15 cm)	1.00	Deming & Carpenter (2008)	(REC)
Mediterranean (Thyrrenian Sea)	3526	^{3}H-thymidine	20 nM	12 hours	production	56.3 ± 27.7 ng C l^{-1} h^{-1}	47.6 ± 14.3 ng C l^{-1} h^{-1}	near bottom water	1.18	Danovaro et al. (2008)	

Mediterranean (Thyrrenian Sea)	3526	^{3}H-thymidine	20 nM	12 hours	production	68.2 ± 16.4 ng C l^{-1} h^{-1}	68.3 ± 18.0 ng C l^{-1} h^{-1}	near bottom water	1.00	Danovaro et al. (2008)	
NW Mediterranean (ANTARES)	2400	^{3}H-thymidine	20 nM	6 hours	production	9.71 ± 0.58 ng C g^{-1} h^{-1}	10.93 ± 0.80 ng C g^{-1} h^{-1}	sediments	0.88	Danovaro et al. (2008)	(REC)
Mediterranean (Thyrrenian Sea)	3000	^{3}H-leucine	10 nM	12 hours	production	1.31 ± 0.01 ng C l^{-1} h^{-1}	0.51 ± 0.056 ng C l^{-1} h^{-1}	stratified	2.55	Tamburini et al. (2009)	
Mediterranean (Thyrrenian Sea)	3000	^{3}H-leucine	10 nM	12 hours	production	1.707 ± 0.172 ng C l^{-1} h^{-1}	0.20 ± 0.58 ng C l^{-1} h^{-1}	stratified	8.35	Tamburini et al. (2009)	
Mediterranean (Thyrrenian Sea)	3000	^{3}H-leucine	10 nM	12 hours	production	8.99 ± 1.14 ng C l^{-1} h^{-1}	0.82 ± 0.42 ng C l^{-1} h^{-1}	stratified	10.87	Tamburini et al. (2009)	
Mediterranean (Thyrrenian Sea)	3000	^{14}C-HCO_3^-	40 µM	72 hours	Dark CO_2 fixation	1.80 ± 0.20 ng C l^{-1} h^{-1}	3.00 ± 0.37 ng C l^{-1} h^{-1}	stratified	0.60	Tamburini et al. (2009)	
Mediterranean (Thyrrenian Sea)	3000	^{14}C-HCO_3^-	40 µM	72 hours	Dark CO_2 fixation	16.92 ± 3.35 ng C l^{-1} h^{-1}	7.43 ± 3.71 ng C l^{-1} h^{-1}	stratified	2.30	Tamburini et al. (2009)	
Mediterranean (Thyrrenian Sea)	3000	MCA-leu	10 nM	10 hours	aminopeptidase (Vmax)	1.07 ± 0.06 nM h^{-1}	0.63 ± 0.05 nM h^{-1}	stratified	1.70	Tamburini et al. (2009)	
Mediterranean (Thyrrenian Sea)	3000	MCA-leu	10 nM	10 hours	aminopeptidase (Vmax)	2.84 ± 0.06 nM h^{-1}	1.42 ± 0.13 nM h^{-1}	stratified	2.00	Tamburini et al. (2009)	
Mediterranean (Thyrrenian Sea)	3000	MUF-phosphate	10 nM	10 hours	phosphatase (Vmax)	2.16 ± 0.22 nM h^{-1}	1.35 ± 0.10 nM h^{-1}	stratified	1.60	Tamburini et al. (2009)	
Mediterranean (Thyrrenian Sea)	3000	MUF-phosphate	10 nM	10 hours	phosphatase (Vmax)	7.12 ± 0.22 nM h^{-1}	3.32 ± 0.16 nM h^{-1}	stratified	2.10	Tamburini et al. (2009)	
Mediterranean (Thyrrenian Sea)	3000	MUF-phosphate	10 nM	10 hours	phosphatase (Vmax)	9.31 ± 0.87 nM h^{-1}	1.60 ± 0.21 nM h^{-1}	stratified	5.80	Tamburini et al. (2009)	
Mediterranean (Thyrrenian Sea)	3000	MUF-phosphate	10 nM	10 hours	phosphatase (Vmax)	0.73 ± 0.01 nM h^{-1}	0.53 ± 0.03 nM h^{-1}	stratified	1.40	Tamburini et al. (2009)	
NW Mediterranean (DYFAMED-POTES)	2000	^{3}H-EPS	1,5 µM	24 hours	substrate incorporation	21.57 ± 1.08 pM h^{-1}	19.42 ± 3.62 pM h^{-1}	stratified	1.39	Boutrif et al (2011)	
NW Mediterranean (DYFAMED-POTES)	2000	^{3}H-leucine	10 nM	10 hours	production	1.58 ± 0.16 ng C l^{-1} h^{-1}	0.94 ± 0.09 ng C l^{-1} h^{-1}	stratified	1.44	Boutrif (2012)	
NW Mediterranean (DYFAMED-POTES)	2000	^{3}H-glucose	2 nM	8 hours	substrate incorporation	0.073 ± 0.015 pM h^{-1}	0.0035 ± 0.01 pM h^{-1}	stratified	21	Boutrif (2012)	
NW Mediterranean (ANTARES site)	2000	^{3}H-EPS	1,5 µM	24 hours	substrate incorporation	4.72 ± 0.9 pM h^{-1}	4.3 ± 1 pM h^{-1}	mixed	1.11	Boutrif (2012)	
NW Mediterranean (ANTARES site)	2000	^{3}H-leucine	10 nM	10 hours	production	0.38 ± 0.05 ng C l^{-1} h^{-1}	0.17 ± 0.0 ng C l^{-1} h^{-1}	stratified	2.21	Boutrif (2012)	
NE Atlantic (PAP site)	2000	^{3}H-EPS	1,5 µM	24 hours	substrate incorporation	0.62 ± 0.08 pM h^{-1}	0.73 ± 0.05 pM h^{-1}	stratified	0.85	Boutrif (2012)	
NE Atlantic (PAP site)	3000	^{3}H-EPS	1,5 µM	24 hours	substrate incorporation	0.52 ± 0.15 pM h^{-1}	0.11 ± 0.07 pM h^{-1}	stratified	4.55	Boutrif (2012)	
NE Atlantic (PAP site)	2000	^{3}H-glucose	2 nM	8 hours	substrate incorporation	1.63 ± 0.92 pM h^{-1}	0.35 ± 0.02 pM h^{-1}	stratified	4.63	Boutrif (2012)	
NE Atlantic (PAP site)	3000	^{3}H-leucine	10 nM	12 hours	production	0.11 ± 0.01 ng C l^{-1} h^{-1}	0.035 ± 0.01 ng C l^{-1} h^{-1}	stratified	3.18	Boutrif (2012)	
NE Atlantic (PAP site)	2000	^{3}H-leucine	10 nM	10 hours	production	0.25 ± 0.05 ng C l^{-1} h^{-1}	0.24 ± 0.01 ng C l^{-1} h^{-1}	stratified	1.05	Boutrif (2012)	
NE Atlantic (PAP site)	2000	^{3}H-leucine	10 nM	10 hours	production	0.12 ± 0.04 ng C l^{-1} h^{-1}	0.05 ± 0.0 ng C l^{-1} h^{-1}	stratified	2.32	Boutrif (2012)	
NE Atlantic (PAP site)	2000	^{3}H-leucine	100 pM	5.5 hours	production	0.44 ± 0.16 ng C l^{-1} h^{-1}	0.24 ± 0.02 ng C l^{-1} h^{-1}	stratified	1.83	Boutrif (2012)	
NE Atlantic (PAP site)	500	^{3}H-leucine	10 nM	10 hours	production	0.17 ± 0.002 ng C l^{-1} h^{-1}	0.16 ± 0.022 ng C l^{-1} h^{-1}	stratified	1.05	Boutrif (2012)	
NE Atlantic (PAP site)	1000	^{3}H-leucine	10 nM	10 hours	production	0.20 ± 0.005 ng C l^{-1} h^{-1}	0.24 ± 0.016 ng C l^{-1} h^{-1}	stratified	0.86	Boutrif (2012)	
NE Atlantic (PAP site)	2000	^{3}H-leucine	10 nM	10 hours	production	0.04 ± 0.001 ng C l^{-1} h^{-1}	0.03 ± 0.005 ng C l^{-1} h^{-1}	stratified	1.37	Boutrif (2012)	
NE Atlantic (PAP site)	2000	MUF-phosphate	5 µM	10 hours	phosphatase (Vmax)	9.37 ± 1.31 nM h^{-1}	4.13 ± 0.24 nM h^{-1}	stratified	2.27	Boutrif (2012)	
NE Atlantic (PAP site)	2000	MUF-phosphate	5 µM	10 hours	phosphatase (Vmax)	7.02 ± 0.18 nM h^{-1}	3.10 ± 0.12 nM h^{-1}	stratified	2.27	Boutrif (2012)	
NE Atlantic (PAP site)	2000	MCA-leu	5 µM	10 hours	aminopeptidase (Vmax)	0.21 ± 0.01 nM h^{-1}	0.09 ± 0.01 nM h^{-1}	stratified	2.24	Boutrif (2012)	
NW Mediterranean (Gulf of Lion)	1400	^{3}H-EPS	1,5 µM	24 hours	substrate incorporation	5.32 ± 1.62 pM h^{-1}	5.75 ± 1.07 pM h^{-1}	mixed	0.93	Boutrif (2012)	
NW Mediterranean (Gulf of Lion)	2400	^{3}H-EPS	1,5 µM	24 hours	substrate incorporation	13.87 ± 0.15 pM h^{-1}	17.65 ± 1.51 pM h^{-1}	mixed	0.8	Boutrif (2012)	
NW Mediterranean (ANTARES)	2000	^{3}H-leucine	10 nM	10 hours	production	0.54 ± 0.05 ng C l^{-1} h^{-1}	0.12 ± 0.05 ng C l^{-1} h^{-1}	stratified	4.64	Boutrif (2012)	
NW Mediterranean (ANTARES)	2400	^{3}H-leucine	10 nM	10 hours	production	0.66 ± 0.10 ng C l^{-1} h^{-1}	0.09 ± 0.01 ng C l^{-1} h^{-1}	stratified	7.00	Boutrif (2012)	
NW Mediterranean (Gulf of Lion)	1400	^{3}H-leucine	10 nM	10 hours	production	1.59 ± 0.11 ng C l^{-1} h^{-1}	1.52 ± 0.07 ng C l^{-1} h^{-1}	mixed	1.05	Boutrif (2012)	
NW Mediterranean (Gulf of Lion)	2346	^{3}H-leucine	10 nM	10 hours	production	2.24 ± 0.11 ng C l^{-1} h^{-1}	2.42 ± 0.14 ng C l^{-1} h^{-1}	near bottom water	0.93	Boutrif (2012)	
NW Mediterranean (Gulf of Lion)	2000	^{3}H-leucine	10 nM	10 hours	production	0.12 ± 0.10 ng C l^{-1} h^{-1}	0.07 ± 0.10 ng C l^{-1} h^{-1}	mixed	1.69	Boutrif (2012)	
NW Mediterranean (Gulf of Lion)	2644	^{3}H-leucine	10 nM	10 hours	production	0.62 ± 0.25 ng C l^{-1} h^{-1}	0.93 ± 0.25 ng C l^{-1} h^{-1}	near bottom water	0.66	Boutrif (2012)	
NW Mediterranean (Gulf of Lion)	1800	^{3}H-leucine	10 nM	10 hours	production	0.10 ± 0.03 ng C l^{-1} h^{-1}	0.24 ± 0.01 ng C l^{-1} h^{-1}	mixed	0.41	Boutrif (2012)	
NW Mediterranean (Gulf of Lion)	1943	^{3}H-leucine	10 nM	10 hours	production	0.01 ± 0.00 ng C l^{-1} h^{-1}	0.01 ± 0.00 ng C l^{-1} h^{-1}	near bottom water	1.01	Boutrif (2012)	
NW Mediterranean (Gulf of Lion)	2000	^{3}H-leucine	10 nM	10 hours	production	1.04 ± 0.11 ng C l^{-1} h^{-1}	0.59 ± 0.05 ng C l^{-1} h^{-1}	mixed	1.78	Boutrif (2012)	
NW Mediterranean (Gulf of Lion)	2352	^{3}H-leucine	10 nM	10 hours	production	0.44 ± 0.03 ng C l^{-1} h^{-1}	0.48 ± 0.03 ng C l^{-1} h^{-1}	near bottom water	0.90	Boutrif (2012)	

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