Citation for published version:

María Aranguren-Gassis, Pablo Serret, Emilio Fernández, Juan L. Herrera, Jose F. Domínguez, Valesca Pérez, Jose Escanez. Balanced plankton net community metabolism in the oligotrophic North Atlantic subtropical gyre from Lagrangian observations. *Deep Sea Research Part I: Oceanographic Research Papers*, Volume 68, 2012, Pages 116-122, https://doi.org/10.1016/j.dsr.2012.06.004

Accepted Manuscript

General rights:

RESEARCH HIGHLIGHTS

Lagrangian sampling allows characterizing short time scale NCP variability in Open Ocean

Microbial plankton metabolism in the oligotrophic open ocean tends to be balanced

Calculation of confidence intervals is a useful tool for NCP variability analysis

1   Balanced plankton net community metabolism in the oligotrophic North Atlantic

2   subtropical gyre from Lagrangian observations

3

4   María Aranguren-Gassis[1]; Pablo Serret[1]; Emilio Fernández[1]; Juan L. Herrera[2]; Jose F.

5   Domínguez[3]; Valesca Pérez[4]; Jose Escanez[3].

6   1   Universidad de Vigo, Departamento de Ecología y Biología Animal, Carretera Colegio Universitario

7   s/n, 36310, Vigo, Pontevedra, Spain.

8   2   Universidad de Vigo, Departamento de Física Aplicada, Carretera Colegio Universitario s/n, 36310,

9   Vigo, Pontevedra, Spain

10   3   Instituto Español de Oceanografía. Centro Oceanográfico de Canarias. Vía transversal. Dársena

11   pesquera. 38180. Santa Cruz de Tenerife, Canarias, Spain.

12   4   Centro de Investigación e Información Ambiental - CINAM de Lourizán, de la Consellería de Medio

13   Ambiente e Desenvolvemento Sostible, Xunta de Galicia. Carretera de Marín km. 4, Apdo. 127, 36080,

14   Pontevedra, Spain.

15

16   Corresponding author: Universidad de Vigo, Departamento de Ecología y Biología Animal, Carretera

17   Colegio Universitario s/n, 36310, Vigo, Pontevedra, Spain. Tel.: +34 986814087; fax: +34 986812556

18   Author e-mail address: aranguren@uvigo.es (M. Aranguren-Gassis)

19

20

21

ABSTRACT

Characterization of the microbial plankton metabolism in oligotrophic oceans is of relevance for the quantification of the global carbon balance; however whether the plankton community metabolism in oligotrophic gyres is net autotrophic or heterotrophic is still under debate. Discrepancies have been in part attributed to the difficulties of the standard snapshot estimations, based on *in vitro* measurements, to adequately represent the temporal scale of trophic processes. This work presents concurrent measurements of gross primary production and community respiration carried out in the North Atlantic Oligotrophic Gyre throughout two 7 days Lagrangian experiments that allowed us to investigate the effect of short term (daily) variability on the microbial metabolism quantification. Physicochemical and biological variables showed a low variability in each Lagrangian experiment and a balanced net plankton metabolism was found in 83% of the sampling days.

1. INTRODUCTION

Oligotrophic gyres are extensive, low productivity oceanic regions whose metabolic balance is still under debate. They cover about 60% of the total ocean surface and their contribution to the global ocean organic carbon pump is higher than 50% (Emerson *et al.* 1997). In addition recent observations of the expansion of low-chlorophyll oceanic regions have been related to global warming (Polovina *et al.* 2008). The role of subtropical oligotrophic gyres in the global metabolic balance of the oceans is nevertheless controversial. Many studies based on incubation measurements have repeatedly reported a net heterotrophic microbial metabolism in oligotrophic waters (e.g. Aranguren-Gassis *et al.* 2011; Duarte and Agustí 1998; Duarte *et al.* 2001; Robinson *et al.* 2002; Serret *et al.* 2001; Morán *et al.* 2004; Williams *et al.* 2004) while others have estimated net autotrophic metabolism (e.g. Williams 1998; Williams and Purdie 1991; Serret *et al.* 2006). In these studies, net community production values (NCP, the difference between gross primary production and community respiration) are usually the mean of 4-6 replicated measurements, typically presented with their corresponding standard error. These data are assumed to indicate net heterotrophy whenever the magnitude of NCP is lower than zero or net autotrophy when NCP is higher than zero. Such assumption implies that very few (or none) NCP data would be indicative of a balanced community metabolism, because they would be required to be zero, typically to the decimal place of the O_2 concentration in mmol m^{-3}. The potential bias of this form of data analysis may increase the disagreements between different studies, particularly in the oligotrophic open ocean, where production and respiration rates are very low, and positive and negative NCP values are usually not far from zero. Here we propose a classification of the net metabolic data based on their statistical significance according to their corresponding 95% confidence interval (C.I.), with communities classified as balanced whenever the C.I. of

63 the mean NCP includes the zero, and as net auto- or heterotrophic only when the mean NCP is

64 higher or lower than zero (respectively) and the corresponding C.I. does not include the zero.

65   The above mentioned discrepancies about the metabolic balance in oligotrophic

66 systems have been partially attributed to the low temporal resolution in published studies of *in*

67 *vitro* metabolic rates, usually designed to provide regional or annual descriptions (Arístegui

68 and Harrison 2002; Karl *et al.* 2003; Williams 2004). However, responses to environmental

69 changes of both autotrophic and heterotrophic components of the oligotrophic plankton

70 communities have been observed to occur over short, daily, time scales (Martínez-García *et*

71 *al.* 2010; Moore *et al.* 2008; Pulido-Villena *et al.* 2008). Such variability could then bias

72 estimates of the microbial metabolic balance derived from low resolution snapshot sampling

73 (Karl *et al.* 2003).

74   An alternative is the sequential sampling of the same water body. However, adequate

75 tracking of water bodies presents several challenges. Either drogued drifter buoys or tracers

76 injected into the ocean surface can be altered by physical processes like wind and wave

77 forces, horizontal advection, vertical shearing or diffusion (Niiler *et al.* 1987; Stanton *et al.*

78 1998). These technical problems and the associated expensive operations make Lagrangian

79 observations sparse (Davis 1991) which prevents an adequate characterization of the

80 microbial plankton metabolism over short-time scales, especially in remote regions such as

81 the oligotrophic gyres. Published Lagrangian studies determining microbial production and

82 respiration rates are mostly focussed on episodic highly productive pulses (Arístegui and

83 Harrison, 2002; Williams 2000). We only found one Lagrangian study, conducted as part of

84 the PRIME project cruise, in the oligotrophic Atlantic ocean (Donald *et al.* 2001; Joint *et al.*

85 2001; Savidge and Williams 2001), but its low vertical resolution did not allow to estimate the

86 metabolic balance of the photic zone. We have measured daily primary production and

87 respiration rates during 7 consecutive days in two Lagrangian experiments carried out in the

88   North Atlantic Subtropical Gyre. The direct monitoring of the time evolution of the microbial

89   metabolic balance of particular water bodies allows us to explore the influence of short-term

90   scale (daily) variability on the quantification of the microbial metabolic balance of the

91   oligotrophic ocean. As far as we are aware, these are the first Lagrangian experiments

92   conducted in oligotrophic open ocean waters not focused on any mesoscale structure or

93   episodic productive event where both autotrophic and heterotrophic rates have been

94   simultaneously measured over daily time scales.

95   The objectives of this investigation were to improve estimates of the net metabolic

96   balance of plankton communities in the oligotrophic open ocean and to elucidate if the

97   temporal resolution of snapshot measurements influences NCP estimates.

98

2. METHODS

2.1. Study area and Lagrangian drifter

Two 7 days Lagrangian experiments were carried out in the North Atlantic Subtropical Gyral Province East (NASTE) in October – November 2006 on board of R.V. *Hespérides* as part of the CARPOS cruise. Sampling for the first Lagrangian experiment (L1) was located at 36.6ºW - 25ºN and lasted from 24 October to 31 October. Fourteen days later, from 14 November to 21 November, the second Lagrangian experiment (L2) sampling was carried out at 26.3ºW - 24.8ºN (Fig. 1).

A drifting buoy was used to follow the selected water bodies. The deployment locations were chosen on the basis of the thermohaline and current velocity fields analyzed one day before the beginning of each experiment in two 100x100 km mesoscale areas. A SBE25 CTD probe and a vessel-mounted Acoustic Doppler Current Profiler (VM-ADCP) were used to characterize the dynamic field. On each experiment, the release locations were selected to avoid the drifter from leaving the mesoscale area. Figure 2 shows the spatial distribution of the averaged temperature between 10 and 30m depth measured during the mesoscale surveys. Temperature data were interpolated with statistical optimal interpolation method into an even longitude–latitude 0.04° grid (see Thiébaux and Pedder, 1987 and Gomis *et al.* 2001 for computational details). Then, the thermal fields were smoothed using a normal error filter (Gomis *et al.* 2002) with a cut-off wavelength twice the mean separation distance among stations.

The drifting buoy was equipped with satellite communication and GPS systems. GPS fixes were stored in a data-logger every 10 seconds. The mooring line included a downward looking RDI 300 kHz Workhorse Self-contained Acoustic Doppler Current Profiler (SC-ADCP) at 2m depth and a drogue at ca. 25m depth. The SC-ADCP data was used to measure the drifter slip and by this means the proper performance of the drifter was monitored.

124

2.2. Sampling and hydrographic characterization

Sampling was always carried out next (<250m) to the Lagrangian buoy. Sampling was

conducted on 81 occasions (38 and 43 for L1 and L2 respectively), both during day and night.

Sampling times were spaced from 1 to 12h each other. At each time, vertical profiles of

temperature and conductivity were carried out with a Seabird 911plus CTD probe. Data were

processed using software provided by the manufacturer following UNESCO

recommendations (UNESCO technical papers 1988). The CTD probe was calibrated by the

manufacturer just before the cruise. Vertical irradiance profiles were made at midday with a

Satlantic ICP-100 FF radiometer.

Water samples for chemical and biological analysis were drawn from 6-11 discrete

depths between 0 and 300m with 20 l Niskin bottles rosette fitted to the CTD.

136

2.3. Nitrate plus nitrite concentration

15 ml water samples were collected in stoppered polypropylene conical centrifuge

tubes. Samples for nanomolar analysis of NO_3 and NO_2 were fitted directly onto the

AutoSampler of a six channels Technicon — Bran Luebbe AA II AutoAnalyzer for

determination by Continuous Flow Analysis using the method described in Raimbault *et al.*

(1990). Samples for the analysis of micromolar concentration of NO_3 and NO_2 were frozen

and stored for the subsequent analysis at the laboratory following the methodology described

in Tréguer and Le Corre (1975).

The depth of the nitracline was calculated by linear interpolation and taken as the

depth where the value of 1 mmol m^{-3} $NO_3 + NO_2$ concentration was reached (Campbell and

Vaulot 1993).

148

2.4. Chlorophyll-a

Fluorescence was measured with a SeaPoint fluorometer fitted to the CTD. Fluorescence data were converted to chlorophyll-a units through the calibration with simultaneous chlorophyll-a measurements made on acetone extracts from filtered water samples (chlorophyll = 0.94 fluorescence + 0.05; r^2 = 0.76; p<0.001; n = 389). For those chlorophyll-a measurements 250ml water samples were sequentially filtered through 2 μm and 0.2 μm pore size polycarbonate filters. Chlorophyll-a was extracted with 5ml of 90% acetone during 12 hours at 4ºC in darkness and measured with a Turner Designs 700 fluorometer calibrated with pure chlorophyll-a standard (Welschmeyer 1994). Total chlorophyll-a was calculated as the sum of the two size fractions.

2.5. Oxygen production and consumption

Oxygen production and consumption rates were estimated daily by *in vitro* changes of dissolved oxygen after 24h light and dark *in situ* incubations. Water samples were taken predawn from 4-5 depths and immediately transferred from the Niskin bottles to 100ml nominal volume borosilicate bottles individually calibrated, overflowing >200ml. Irradiance levels corresponding to 85%, 50%, 11%, 6% and 1% of surface irradiance were calculated from vertical profiles of irradiance conducted the previous day with a Satlantic ICP-100 FF radiometer and the present day deep chlorophyll-a maximum location (Poulton *et al.* 2006; Robinson *et al.* 2006).

For each depth, four dark bottles were fixed immediately for initial oxygen concentration measurement and the rest of the samples (4 in light and 4 in dark bottles) were fixed after 24h incubation, all of them following Grasshoff *et al.* (1999) recommendations. *In situ* incubations were conducted in a buoy located next to the Lagrangian buoy. Bottles were hanged from the incubation buoy at the corresponding sampling depth, with dark bottles

174 inside individual opaque bags. Dissolved oxygen was measured by precision Winkler titration

175 performed with a Metrohm 716 DMS Titrino utilizing a potentiometric end point (Oudot *et al.*

176 1988; Serret *et al.* 1999).

177 Community respiration (CR) was calculated from the difference between the averaged

178 dissolved oxygen concentration in the incubated dark bottles and that in the initial samples.

179 Net community production (NCP) was calculated from the difference between the averaged

180 dissolved oxygen concentration in the incubated light bottles and that in the initial samples.

181 Gross primary production (GPP) was calculated from the difference between the averaged

182 dissolved oxygen concentration in the incubated light bottles and that in the incubated dark

183 bottles.

184 Averaged coefficients of variation of the dissolved oxygen replicates were 0.13, 0.11

185 and 0.13 for zero time, dark and light treatments respectively, and the pooled coefficient of

186 variation (± standard error) was 0.12 ± 0.01 %, similar to previously published values

187 (González *et al.* 2001 and 2002, Morán *et al.* 2004).

188 Photic zone integrated values were calculated by trapezoidal integration of the

189 volumetric data from the surface to depth of the 1% incident irradiance and the standard errors

190 were calculated following the propagation procedures for independent measurements

191 described by Miller and Miller (1988).

192

193

194 # 3. RESULTS

195 ## 3.1 Lagragian drifter and thermohaline vertical distribution

196   Buoy displacement was lower than 5 and 9 Km per day for L1 and L2 respectively,

197 being always located inside the area of the corresponding mesoscale survey. Surface

198 temperature variability in the sampled area was lower than 0.2 ºC during both experiments

199 (Fig. 2). The vertical distribution of temperature (Fig. 3) showed strong stratification and low

200 temporal variation during both Lagrangian experiments. High surface temperature (26 and

201 25ºC for L1 and L2 respectively) and a gradual decrease below 50 m depth were measured at

202 both Lagrangian studies.

203

204 ## 3.2. Nitrate plus nitrite concentration and chlorophyll-a concentration

205   In both Lagrangian studies, NO_3 plus NO_2 concentrations were lower than 0.3 mmol

206 m^{-3} upper to 100 m depth (Fig. 4). The nitracline (1 mmol m^{-3} isoline in Fig. 4, see methods)

207 was located around 140 m depth during both Lagrangian experiments.

208   Chlorophyll-a concentration was lower than 0.2 mg m^{-3} in the upper 50 m during both

209 experiments (Fig. 5). A well developed deep chlorophyll-a maximum (DCM) was located at

210 the base of the photic zone (t-student test with Welch's correction between the averaged depth

211 of the DCM and the averaged depth of the 1% incident irradiance measured, n=15 and n=81

212 respectively; t=1.4; p=0.2) where chlorophyll-a concentrations exceeded 0.3 mg m^{-3}. In

213 general, the nitracline was slightly deeper than the DCM (Fig. 5). Thus, NO_3 plus NO_2

214 concentrations were lower than 1 mmol m^{-3} in the entire photic zone.

215   The averaged pico-phytoplankton (<0.2 μm) contribution to total chlorophyll-a

216 concentration was 66 ± 1 % (mean ± standard error) for the complete data set (n=93), and the

217 highest contribution (>70%) was located at the DCM depth during both experiments.

218

3.3. Planktonic metabolic rates

220   The complete volumetric data set, including the propagated standard error of every

221 measurement, is available at the global respiration data base:

222 http://www.uea.ac.uk/env/people/facstaff/plankton (data compiled and maintained by Carol

223 Robinson initially for Robinson 2008).

224   Photic zone GPP rates (± propagated standard error) varied between 6.5±17.3 and

225 58.7±12.2 mmol O_2 m^{-2} d^{-1}. A similar range was measured for CR, which varied from

226 16±16.8 to 65.1±11.7 mmol O_2 m^{-2} d^{-1}. The 95% confidence intervals (C.I.) were calculated

227 to analyze differences between metabolic rates estimations during the course of each

228 Lagrangian experiment (Fig. 6a and 6b). The averaged rates for GPP were 35.6 and 30.8

229 mmol O_2 m^{-2} d^{-1} during the L1 and L2 experiments respectively, and the averaged rates for

230 CR were 41.4 and 44.9 mmol O_2 m^{-2} d^{-1} during the L1 and L2 experiments respectively. Each

231 day, neither GPP nor CR rates were significantly different from the averaged value of the

232 corresponding Lagrangian experiment.

233   NCP photic depth integrated rates varied between -53.8±14.2 and 18.6±12.5 mmol O_2

234 m^{-2} d^{-1}. Averaged NCP rates were -7.8 and -16 mmol O_2 m^{-2} d^{-1} for L1 and L2 respectively.

235 However, when the 95% confidence intervals (C.I.) were calculated, NCP rates were not

236 significantly different from 0 in all except two sampling days (Fig. 6c and 6d). In L1 at 120h

237 and in L2 at 168h NCP was significantly lower than 0.

238

4. DISCUSSION

Physical, chemical and biological characteristics observed in the upper water column during both Lagrangian experiments were typical of oligotrophic gyre waters, namely: strong stratification with mixed layer depth at around 50 m depth (Longhurst 1998; Marañón *et al.* 2003), a well developed DCM deeper than 60 m depth (Longhurst 1998; Marañón *et al.* 2003), surface chlorophyll-a concentration lower than 0.2 mg m^{-3} (Marañón and Holligan 1999) and dominance of picophytoplankton (Agawin *et al.* 2000), and nitracline deeper than 70 m depth (Marañón *et al.* 2003).

Furthermore temperature vertical distribution presented low variability during both Lagrangian studies as well as nutrient and chlorophyll-a concentration, suggesting a quasi-steady state of the water column. Similar low variation in the physicochemical and biological characteristics was found during a previous Lagrangian study carried out in oligotrophic waters of the NE Atlantic in spring 1996 (Donald *et al.* 2001).

Estimated GPP and CR rates, as well as NCP rates, were in the range of previously published data for the same region (e.g. Aranguren-Gassis *et al.* 2011; Gist *et al.* 2009; Morán *et al.* 2004). Means of the standard errors were 0.20 mmol O$_2$ m^{-3} d^{-1} for CR and GPP and 0.22 mmol O$_2$ m^{-3} d^{-1} for NCP measurements, also within the range of previously published values (Morán *et al.* 2004; Robinson *et al.* 2002; Robinson and Williams, 2005). In addition, we explored the data from the public data base compiled and maintained by Carol Robinson (http://www.uea.ac.uk/env/people/facstaff/plankton data initially for Robinson 2008). If we only consider the NCP rates that are in the range of our NCP data (between -1.1 and 0.4 mmol O$_2$ m^{-3} d^{-1}) the averaged standard error is 0.23 mmol O$_2$ m^{-3} d^{-1}, similar to ours. So the precision of the data from our Lagrangian experiments is comparable to previously published studies that have characterized the plankton metabolic balance from the mean of replicated snapshot measurements. Hence differences in our results do not emerge from differences in

264 the magnitude or precision of the data, but form the consideration of the statistical

265 significance (based on the 95% C.I.) of the mean NCP rates measured to classify the

266 communities as balanced, net auto- or net heterotrophic.

267 When the C.I. for the means are considered, both GPP and CR showed very small

268 changes throughout the 7 sampling days in agreement with the low variability shown by the

269 physical and chemical characteristics of the water column during the experimental periods.

270 None of the GPP and CR photic zone integrated rates were significantly different from the

271 corresponding Lagrangian averaged values and only two sampling days showed differences

272 between CR and GPP high enough as to result in a net heterotrophic metabolism. Altogether,

273 during our Lagrangian experiments NCP rates tended to be balanced. These results contrast

274 with the existing literature about the plankton metabolic balance in oligotrophic systems that

275 has confronted studies supporting the prevalence of net heterotrophy, that is, NCP values

276 lower than zero (e.g. Arístegui and Harrison 2002; Duarte and Agustí 1998; González *et al.*

277 2001, 2002; Serret *et al.* 2001) with others that have found net autotrophy with NCP values

278 greater than zero (e.g. Serret *et al.* 2006; Williams and Purdie 1991). Such a difference results

279 from the use of confidence intervals to classify the community metabolism proposed in this

280 study that allows us a more rigorous analysis of the NCP rates variability.

281 Our results also differ from previous works in the time scale resolution, as the

282 Lagrangian design of our study allows analyzing the NCP variability on a daily-time scale.

283 The prevalence of net balanced metabolism in both one-week Lagrangian studies, located in

284 two distant areas of the oligotrophic gyre, suggest a more widespread net balanced

285 metabolism than previously reported for this region. With the aim to compare the results

286 obtained in this study with those derived from standard snapshot sampling we calculated the

287 probability to estimate a heterotrophic metabolic balance during each of the Lagrangian

288 experiments. If the water bodies analyzed in the present study would be sampled only once, as

289 is the case in most oceanographic cruises, we could expect net heterotrophy to occur in 58%

290 of the cases (7 negative NCP rates out of the 12 days sampled). Net heterotrophy would only

291 prevail in the area located closer to the periphery of the gyre (80% at L2 vs. 42% at L1), in

292 accordance with the potential supply of allochthonous organic matter from the neighbouring

293 productive region (Serret *et al.* 2002 and 2009). However, taking into account the NCP

294 confidence intervals, the general percentage decreases to 17% as only 2 NCP rates were

295 significantly lower than 0, and contrary to net heterotrophy prevalence, 83% of NCP

296 estimations were balanced. This analysis also implies that regional differences fade away,

297 with 20% of net heterotrophic observations at L2 vs. 14% at L1.

298   Karl *et al.* (2003) approximated that, if only one observation is made, the open ocean

299 system would be incorrectly catalogued as net heterotrophic 89% of the times. Those

300 calculations were based on the hypothesis that net heterotrophy in open ocean systems results

301 from the uncoupling between relatively constant heterotrophic processes and pulses of

302 primary production that occurs 10% of the time. These authors proposed that net heterotrophy

303 in these oceanic regions can be sustained by previous autotrophic pulses (Karl *et al.* 2003;

304 Williams *et al.* 2004). During our Lagrangian experiments production and respiration rates

305 were balanced throughout 4 to 6 days previous to the time when the two measurements of net

306 heterotrophic rates were made. Although the 7 days extent of our experiments cannot cover

307 the weekly time scale on which pulses of GPP can occur, the very low variability of the

308 physicochemical and biological characteristics of the sampled water body suggests that the

309 existence of a recent strong positive NCP pulse is an unlikely explanation as to support the

310 heterotrophic rates observed in our experiments.

311   Other authors have also supported the hypothesis that the microbial plankton

312 metabolic balance is controlled by factors controlling GPP, mainly the nutrient concentration

313 (Arístegui and Harrison 2002; González *et al.* 2002), based on the prevalence of net

314 heterotrophy in oligotrophic waters (del Giorgio *et al.* 1997; Duarte and Agustí 1998; Morán

315 *et al.* 2004) together with the observation that GPP variability is frequently higher than CR

316 variability (Duarte *et al.* 2001; González *et al.* 2001; Morán *et al.* 2004). When we focus on

317 the two days when significant net heterotrophy disrupted the prevalence of balanced

318 metabolism in our Lagrangian experiments clear differences were observed. At L1,

319 heterotrophy was related to the lowest GPP rate, in agreement with the GPP control

320 hypothesis. However, during the L2 experiment the net heterotrophic metabolism coincided

321 with the highest CR rate but not with a low GPP, suggesting that NCP variability is not only

322 modulated by GPP changes. These results indicate that variability of CR also plays an

323 important role in the modulation of NCP in the oligotrophic open ocean.

324

325   5. CONCLUSION

326   In conclusion, this is the first time that direct *in situ* measurements of both autotrophic

327 and heterotrophic processes have been conducted in the North Atlantic oligotrophic gyre to

328 estimate the plankton microbial metabolic balance over short time scales allowed by a

329 Lagrangian sampling design. Our results demonstrate the importance of using the confidence

330 interval as a tool to adequately characterize the metabolic balance of the microbial plankton

331 communities. The microbial plankton metabolism in the unproductive open ocean may be

332 more balanced than previously reported, as NCP was not different from 0 in 83% of the

333 sampling days.

334

AKNOWLEDGMENTS

REFERENCES

1. Agawin,N.S.R., C.M.Duarte, and S.Agustí 2000. Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. Limnol. Oceanogr. 45 (3): 591-600

2. Aranguren-Gassis,M., P.Serret, E.Fernández, J.L.Herrera, J.F.Domínguez, V.Pérez and J.Escanez 2011. Production and respiration control the marine microbial metabolic balance in the eastern North Atlantic subtropical gyre. Deep-Sea Res. I 58: 768 - 775.

3. Arístegui,J. and W.G.Harrison 2002. Decoupling of primary production and community respiration in the ocean: implications for regional carbon studies. Aquat. Microb. Ecol. 29: 199-209.

4. Campbell,L. and D.Vaulot 1993. Photosynthetic picoplankton community structure in the subtropical North Pacific Ocean near Hawaii (station ALOHA). Deep-Sea Res. I 40: 2043-2060.

5. Davis,R.E. 1991. Lagrangian ocean studies. Annu. Rev. Fluid Mech. 23: 43-64.

6. del Giorgio,P.A., J.J.Cole, and A.Cimbleris 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385: 148-151.

7. Donald,K.M., I.Joint, A.P.Rees, E.M.S.Woodward, and G.Savidge 2001. Uptake of carbon, nitrogen and phosphorus by phytoplankton along the 20ºW meridian in the NE Atlantic between 57.5ºN and 37ºN. Deep-Sea Res. II 48: 859-897.

8. Duarte,C.M. and S.Agustí 1998. The CO_2 balance of unproductive aquatic ecosystems. Science 281: 234-236.

9. Duarte,C.M., S.Agustí, J.Arístegui, N.González, and R.Anadón 2001. Evidence for a heterotrophic subtropical northeast Atlantic. Limnol. Oceanogr. 46: 425-428.

366 10. Emerson,S., P.Quay, D.Karl, C.Winn, L.Tupas, and M.Landry 1997. Experimental

367 determination of the organic carbon flux from open-ocean surface waters. Nature 389: 951-

368 954.

369 11. Gist,N., P.Serret, E.M.S.Woodward, K.Chamberlain, and C.Robinson 2009. Seasonal and

370 spatial variability in plankton production and respiration in the Subtropical Gyres of the

371 Atlantic Ocean. Deep-Sea Res. II 56: 931-940.

372 12. Gomis,D., M.A.García, , L.Oswaldo, , and A.Pascual, 2002. Quasi-geostrophic 3D

373 circulation and mass transport in the western Bransfield Strait during Austral summer

374 1995/1996. Deep-Sea Res. II 49: 603–621.

375 13. Gomis,D., S.Ruiz, and M.A.Pedder, 2001. Diagnostic analysis of the 3-D ageostrophic

376 circulation from a multivariate spatial interpolation of CTD and ADCP data. Deep-Sea Res. I

377 48: 269–295.

378 14. González,N., R.Anadón, and E.Marañón 2002. Large-scale variability of planktonic net

379 community metabolism in the Atlantic Ocean: importance of temporal changes in

380 oligotrophic subtropical waters. Mar. Ecol. Prog. Ser. 233: 21-30.

381 15. González,N., R.Anadón, B.Mouriño, E.Fernández, B.Sinha, J.Escánez, and D.de Armas

382 2001. The metabolic balance of the planktonic community in the North Atlantic Subtropical

383 Gyre: The role of mesoscale instabilities. Limnol. Oceanogr. 46: 946-952.

384 16. Grasshoff,K., K.Kremling, and M.Ehrhardt 1999. Determination of Oxygen, p. 75-89.

385 Chapter 4 *In* K.Grasshoff 1999, Methods of seawater analysis, 3 ed. Wiley-VCH.

386 17. Joint,I., P.J.leB.Williams, and G.Savidge 2001. Comparison of plankton at 59ºN and 37ºN

387 during two Lagrangian drift experiments in the North Atlantic in June and July 1996. Deep-

388 Sea Res. II 48: 1043-1061.

389 18. Karl,D.M., E.A.Laws, P.J.Morris, P.J.leB.Williams, and S.Emerson 2003. Metabolic

390 balance of open sea. Nature 426: 32.

391 19. Longhurst,A.R. 1998. Ecologycal geography of the sea. Academic Press.

392 20. Marañón,E., M.J.Behrendfeld, N.González, and B.Mouriño 2003. High variability of

393 primary production in oligotrophic waters of the Atlantic Ocean: uncoupling from

394 phytoplankton biomass and size structure. Mar. Ecol. Prog. Ser. 257: 1-11.

395 21. Marañón,E. and P.M.Holligan 1999. Photosynthetic parameters of phytoplankton from

396 50ºN to 50ºS in the Atlantic Ocean. Mar. Ecol. Prog. Ser. 176: 191-203.

397 22. Martínez-García,S., E.Fernández, A.Calvo-Díaz, E.Marañón, X.A.G.Morán and E.Teira

398 2010. Response of heterotrophic and autotrophic microbial plankton to inorganic and organic

399 inputs along a latitudinal transect in the Atlantic Ocean. Biogeosciences 7: 1701-1713

400 23. Miller,J.N. and J.C.Miller 1988. Statistics for Analytical Chemistry, 2nd ed. Ellis

401 Horwood Limited.

402 24. Moore,C.M., M.M.Mills, R.Langlois, A.Milne, E.P.Achterberg, J.La Roche and

403 R.J.Geider 2008. Relative influence of nitrogen and phosphorus availability on phytoplankton

404 physiology and productivity in the oligotrophic sub-tropical North Atlantic Ocean. Limnol.

405 Oceanogr. 53: 291-305

406 25. Morán,X.A.G., E.Fernández, and V.Pérez 2004. Size-fractionated primary production,

407 bacterial production and net community production in subtropical and tropical domains of the

408 oligotrophic NE Atlantic in autumn. Mar. Ecol. Prog. Ser. 274: 17-29.

409 26. Niiler,P.P., R.E.Davis, and H.J.White 1987. Water-following characteristics of a mixed

410 layer drifter. Deep-Sea Res. 34: 1867-1881.

411 27. Oudot,C., R.Gerard, P.Morin, and I.Gningue 1988. Precise shipboard determination of

412 dissolved oxygen (Winkler procedure) for productivity studies with a commercial system.

413 Limnol. Oceanogr. 33: 146-150.

414 28. Polovina,J.J., E.A.Howell, and M.Abecassis 2008. Ocean's least productive waters are

415 expanding. Geophys. Res. Lett. 35: L03618. doi:10.1029/2007GL031745.

416 29. Poulton,A.J., P.M.Holligan, A.Hickman, Y.-N.Kim, T.R.Adey, M.C.Stinchcombe, C.Holeton, S.Root, and E.M.Woodward 2006. Phytoplankton carbon fixation, chlorophyll-biomass and diagnostic pigments in the Atlantic Ocean. Deep-Sea Res. II 53: 1593-1610.

419 30. Pulido-Villena,E., T.Wagener, and C.Guieu 2008. Bacterial response to dust pulses in the western Mediterranean: Implications for carbon cycling in the oligotrophic ocean. Global Biogeochem. Cycles 22: GB1020. doi:10.1029/2007GB003091.

422 31. Raimbault, P., G.Slawyk, B.Coste and J.Fry 1990. Feasibility of using an automated colorimetric procedure for the determination of seawater nitrate in the 0 to 100 ηM range: examples from field and culture. Mar. Biol. 104: 347-351.

425 32. Robinson,C. 2008. Heterotrophic bacterial respiration, p. 299-334. Chapter 9 *In* D.L.Kirchman 2008, Microbial Ecology of the Oceans. John Wiley and Sons, Inc.

427 33. Robinson,C., A.J.Poulton, P.M.Holligan, A.R.Baker, G.Forster, N.Gist, T.D.Jickells, G.Malin, R.Upstill-Goddard, R.G.Williams, E.M.S.Woodward, and M.V.Zubkov 2006. The Atlantic Meridional Transect (AMT) Programme: A contextual view 1995-2005. Deep-Sea Res. II 53: 1485-1515.

431 34. Robinson,C. and P.J. leB.Williams 2005. Respiration and its measurement in surface marine waters, p.147-179. Chapter 9 *In* P.A.del Giorgio and P.J.leB.Williams 2005. Respiration in aquatic ecosystem, 1 ed. Oxford University.

434 35. Robinson,C., P.Serret, G.Tilstone, E.Teira, M.V.Zubkov, A.P.Rees, and E.M.Woodward 2002. Plankton respiration in the Earsten Atlantic Ocean. Deep-Sea Res. I 49: 787-813.

436 36. Savidge,G. and P.J.leB.Williams 2001. The PRIME 1996 cruise: an overview. Deep-Sea Res. II 48: 687-704.

438 37. Serret,P., C.Robinson, E.Fernández, E.Teira, G.Tilstone, and V.Pérez 2009. Predicting plankton net community production in the Atlantic Ocean. Deep-Sea Res. II 56: 941-953.

440   38. Serret,P., E.Fernández, and C.Robinson 2002. Biogeographic differences in the net ecosystem metabolism of the open ocean. Ecology 83: 3225-3234.

442   39. Serret,P., E.Fernández, C.Robinson, E.M.S.Woodward and V.Pérez 2006. Local production does not control the balance between plankton photosynthesis and respiration in the open Atlantic Ocean. Deep-Sea Res. II 53: 1611-1628

445   40. Serret,P., E.Fernández, J.A.Sostres, and R.Anadón 1999. Seasonal compensation of microbial production in a temperate sea. Mar. Ecol. Prog. Ser. 187: 43-57.

447   41. Serret,P., C.Robinson, E.Fernández, E.Teira, and G.Tilstone 2001. Latitudinal variation of the balance between plankton photosynthesis and respiration in the eastern Atlantic Ocean. Limnol. Oceanogr. 46: 1642-1652.

450   42. Sokal,R.R. and Rohlf,F.J. 1995. Biometry: the principles and practice of statistics in biological research, 3 ed. W.H. Freeman and Company, cop.

452   43. Stanton,T.P., C.S.Law, and A.J.Watson 1998. Physical evolution of the IronEx-I open ocean tracer path. Deep-Sea Res. II 45: 947-975.

454   44. Tréguer,P. and P.Le Corre 1975. Manuel d'analyse des sels nutritifs dans l'eau de mer. Utilisation de l'autoanalyseur Technicon II. 2 ed. Loc. Univ. Bretagne Occidentale, Brest.

456   45. Thiébaux,H.J., and M.A.Pedder 1987. Spatial Objective Analysis with Applications in Atmospheric Sciences. Academic Press, pp.299.

458   46. UNESCO, 1988. The UNESCO Technical Papers: The acquisition, calibration, and analysis of CTD data. UNESCO Technical Papers in Marine Sciences, 51.

460   47. Welschmeyer,N.A. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. Limnol. Oceanogr. 39: 1985-1992.

462   48. Williams,P.J.leB. 1998. The balance of plankton respiration and photosynthesis in the open oceans. Nature 394: 55-57.

464   49. Williams,P.J.leB., P.J.Morris, and D.M.Karl 2004. Net community production and

465   metabolic balance at the oligotrophic ocean site, station ALOHA. Deep-Sea Res. I 51: 1563-

466   1578.

467   50. Williams,P.J.leB. 2000. Net production, gross production and respiration; what are the

468   interconnections and what controls what? p. 37-60. Chapter 3 *In* R.B.Hanson, H.W.Ducklow,

469   and J.G.Field 2000, The changing ocean carbon cycle. Cambridge University Press.

470   51. Williams,P.J.leB. and D.A.Purdie 1991. *In vitro* and *in situ* derived rates of gross

471   production, net community production and respiration of oxygen in the oligotrophic

472   subtropical gyre of the North Pacific Ocean. Deep-Sea Res. 38: 891-910.

Fig.1: Location of the Lagrangian studies stations (black crosses) superimposed on a map of monthly averaged surface chlorophyll concentration (mg m^{-3}) in November 2006. Data were obtained from the ocean color website (http://oceancolor.gsfc.nasa.gov/) level-3 products (MODIS-aqua mission) with 9 Km resolution. Lagrangian studies were carried out at the end of October (from 24th to 31st) and November (from 14th to 21st) for L1 and L2 respectively. A colour version of this figure is available in the digital version.

Fig. 2: CTD stations (black points) sampled following the drifter buoys trajectories during the two Lagrangian experiments superimposed on the maps of averaged temperature between 10 and 30m depth measured during the corresponding mesoscale survey (see methods). Grey crosses signal locations with metabolic rates estimations. Grey stars indicate the beginning of the Lagrangian experiment.

Fig. 3: Vertical distribution of temperature (ºC) in the two Lagrangian experiments. Vertical black dotted lines signal sampling times.

Fig. 4: Vertical distribution of $NO_3 + NO_2$ concentration (mmol m^{-3}) in the two Lagrangian experiments. Black points signal sampling times and depths. The thicker white lines are the 1 mmol m^{-3} isoline (see text).

Fig. 5: Vertical distribution of chlorophyll-a concentration (mg m^{-3}) in the two Lagrangian experiments. The dashed white line signals the depth of the nitracline. Vertical black dotted lines signal sampling times. Black stars signal the bottom of the photic layer.

Fig 6: Photic zone integrated values of the metabolic rates (mmol O_2 m^{-2} d^{-1}): (a & b) GPP (solid black line) and CR (dashed light-grey line) and (c & d) NCP (white circles) in both Lagrangian studies. Error bars and grey areas represent the 95% confidence interval for the corresponding rates. Dash-dotted lines represent averaged GPP (black) and CR (grey) during each Lagrangian study.
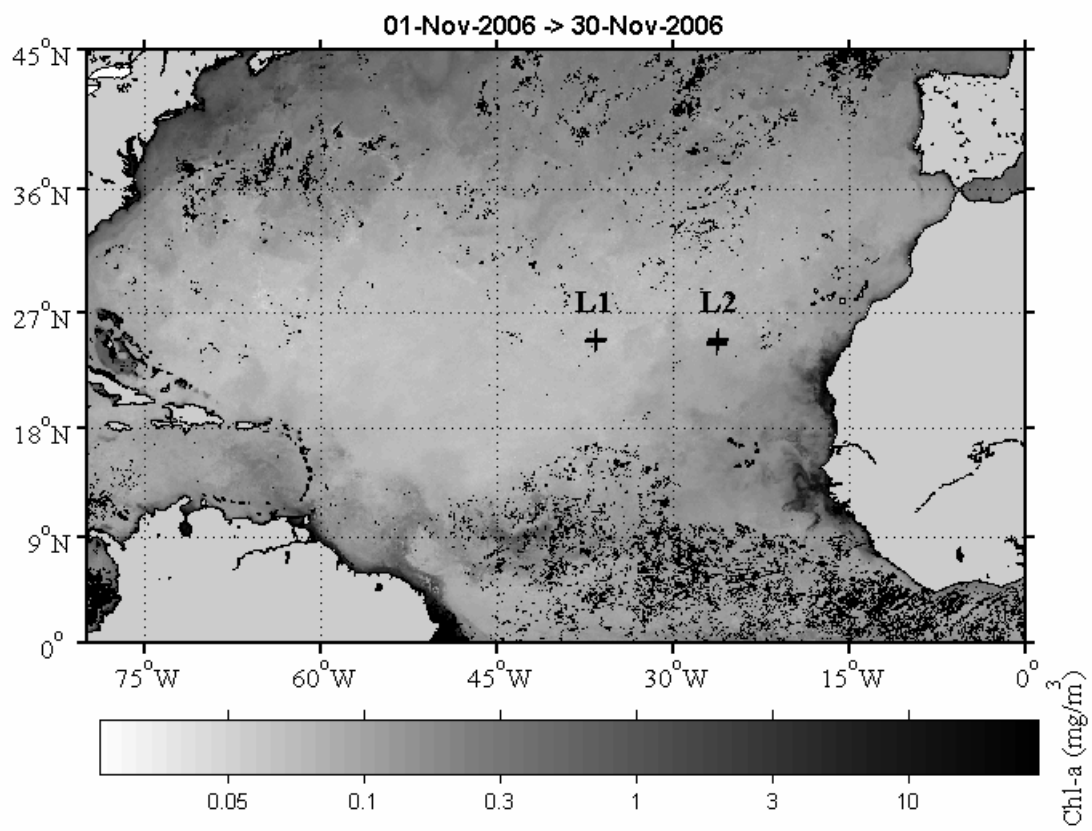
01-Nov-2006 -> 30-Nov-2006

Fig. 1

Figure 2

TEMPERATURE (ºC)

Figure 3

$NO_3 + NO_2$ (mmol m^{-3})

Figure 4

Figure5
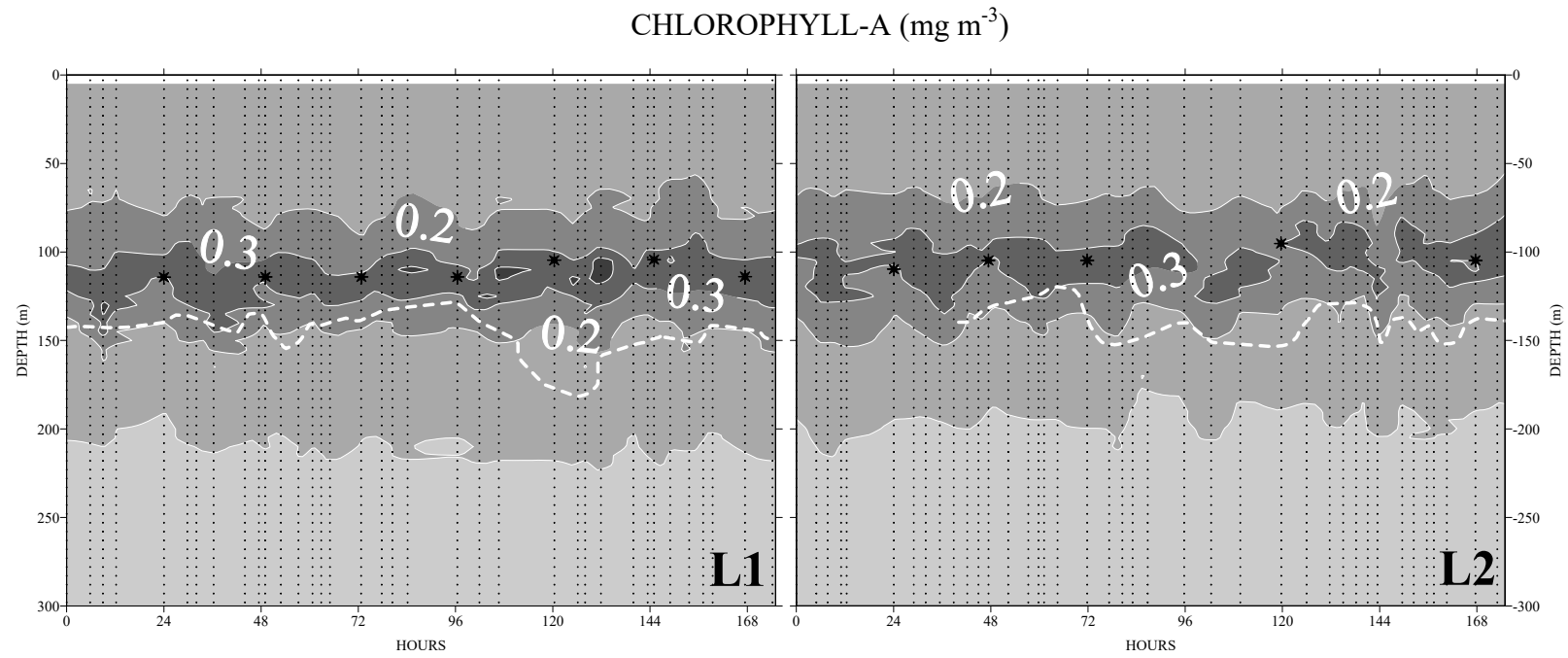**Click here to download Figure: Fig5_revised.pdf**
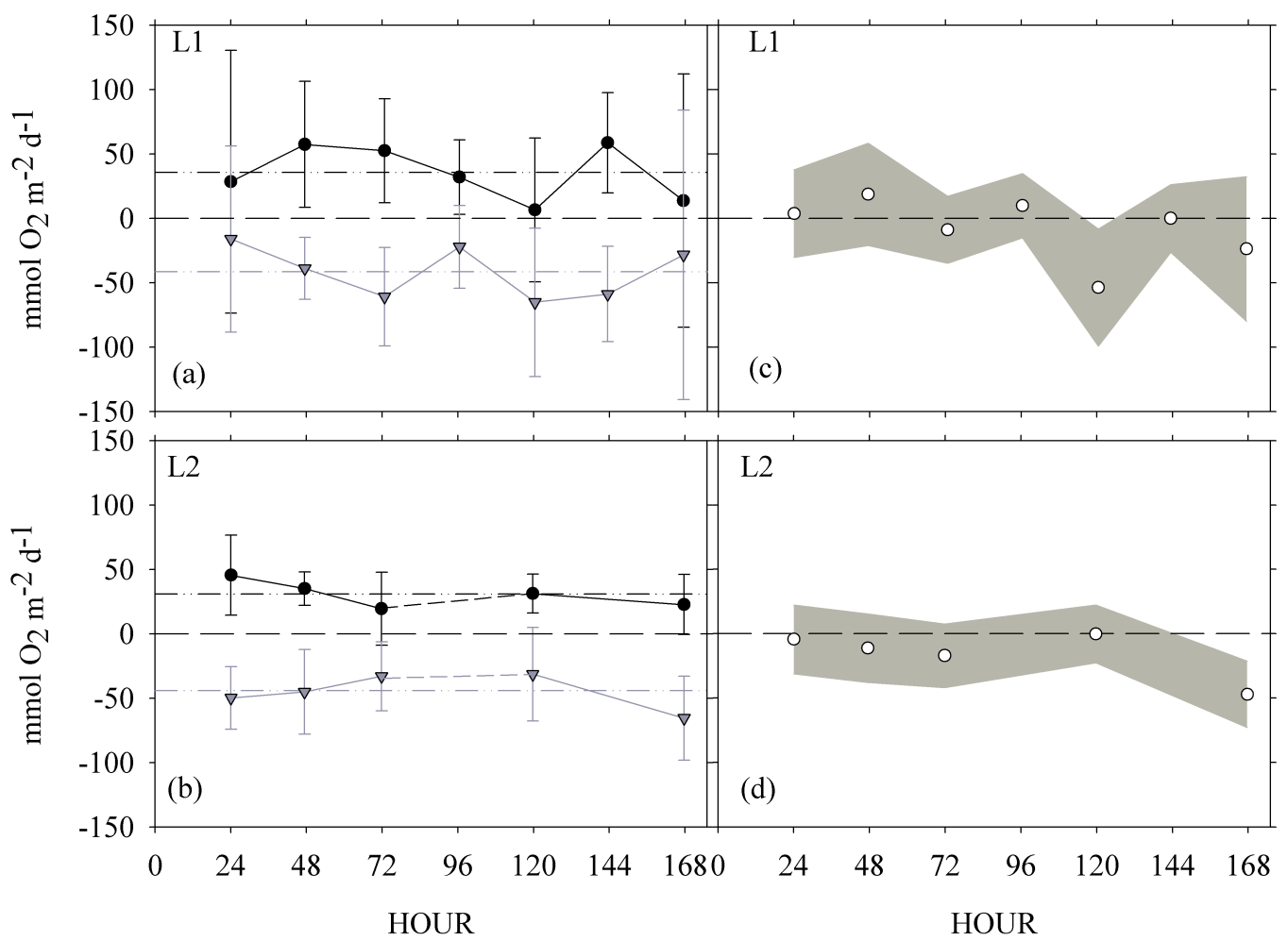
CHLOROPHYLL-A (mg m^{-3})

Figure 5

Figure 6

Color Figure1 for Web

Click here to download Supplementary material: Figure1ColorForWeb_ArangurenGassis.pdf