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Community fluctuations and local extinction in a planktonic food web

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5 1 Community fluctuations and local extinction in a planktonic food web

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50
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53 discussed results. All authors contributed to the writing of the paper.
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5 **Data accessibility statement:**
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7 Station L4 data are archived at the British Oceanographic data centre www.bodc.ac.uk and are freely
8 available upon request to Dr Angus Atkinson aat@pml.ac.uk
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4 12 **Abstract**
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6 13 Determining statistical patterns irrespective of interacting agents (*i.e.* macroecology) is useful to
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8 14 explore the mechanisms driving population fluctuations and extinctions in natural food webs. Here, we
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10 15 tested four predictions of a neutral model on the distribution of community fluctuations (CF) and the
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12 16 distributions of persistence times (APT). Novel predictions for the food web were generated by
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14 17 combining i) body size-density scaling, ii) Taylor's law and iii) low efficiency of trophic transference.
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16 18 Predictions were evaluated on an exceptional dataset of plankton with 15 years of weekly samples
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18 19 encompassing ~250 planktonic species from three trophic levels, sampled in the western English
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20 20 Channel. Highly symmetric non-Gaussian distributions of CF supports zero-sum dynamics. Variability
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22 21 of CF decreased while a change from an exponential to a power-law distribution of APT from basal to
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24 22 upper trophic positions was detected. Results suggest a predictable but profound effect of trophic
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26 23 position on fluctuations and extinction in natural communities.
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34 25 **Key words:** macroecology, plankton, food web, fluctuations, Station L4, English channel
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28 INTRODUCTION

29 The macroecological perspective represents a fruitful and complementary approach to
30 traditional methods in ecology which may provide novel insights on patterns and process shaping
31 biodiversity (John Maynard Smith 1974; Maurer 1999; Harte 2011; Hatton *et al.* 2015). Such a
32 macroscopic approach could be particularly suitable for the analysis of community dynamics involving
33 hundreds of interacting species. The aggregation of population fluctuations $r_s = \log_e(N_{t+1}/N_t)$ of multiple
34 species results in a distribution of community fluctuations (CF) that departs from Gaussian but follows
35 a Laplace probability distribution (Keitt & Stanley 1998):

$$36 \quad P(r_s) = \frac{1}{(2\Phi)} e^{-\frac{|r_s - \mu|}{\Phi}} \quad (\text{eq. 1})$$

37 where μ is the mean and $2\Phi^2$ is the variance (σ_r^2). The distribution extended several orders of
38 magnitude, was symmetric and centered on zero suggesting that demographic gains and losses by all
39 the species were balanced over the study period (Marquet *et al.* 2007). That analysis combined species
40 spanning a wide range of body-sizes feeding at multiple trophic levels. Consistent relationship of
41 trophic position with body size (Arim 2007; Segura *et al.* 2015), and the association of body size with
42 decreased growth rate (Brown *et al.* 2004) increased scale of perception (Ritchie 2010; Borthagaray *et*
43 *al.* 2012) and coupling of energy channels (Rooney *et al.* 2006; Arim *et al.* 2010; Rooney & McCann
44 2012) are expected to drive systematic trends in population fluctuation and trophic position. Moreover,
45 while the propagation of community fluctuations through the food web has been a cornerstone of
46 community ecology (Stouffer & Bascompte 2011; Thompson *et al.* 2012) its connection with the
47 distribution of populations' fluctuation has not been considered so far.

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5 50 The distribution of species aggregated persistence time (APT) has been proposed as a novel
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7 51 macroecological pattern that reflects important ecological processes (Bertuzzo *et al.* 2011; Suweis *et*
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9 52 *al.* 2012). Persistence time of a species was defined as the time span between local colonization and
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11 53 extinction in a given geographic region. APT showed a power-law scaling with exponential cut-off for
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14 54 bird communities and a qualitative relationship between CF and APT was proposed, but no formal link
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16 55 was suggested (Keitt & Stanley 1998). Recently, a formal connection between APT and CF was
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18 56 proposed for neutral systems (Pigolotti *et al.* 2005; Bertuzzo *et al.* 2011). Under neutral dynamics, it
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21 57 was demonstrated that APT distribution followed a power law with an exponential cut-off of the form
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24 58 (Bertuzzo *et al.* 2011):

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$$P(t) \sim t^{-\alpha} e^{-\nu t} \quad (\text{eq. 2})$$

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28 60 When dispersal is unlimited, the scaling exponent (α) equals 2 and $P(t)$ depends solely on the
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31 61 immigration or speciation rate (ν). Ecosystem dimensionality and spatial constraints on dispersal
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33 62 modify the scaling exponent in the range $\alpha=1.5-2$ (Pigolotti *et al.* 2005; Bertuzzo *et al.* 2011) as was
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36 63 observed for breeding birds, herbaceous plants and marine fishes (Bertuzzo *et al.* 2011; Suweis *et al.*
37
38 64 2012). Although the supporting evidence is compelling, the neutral model is limited to explain patterns
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41 65 in trophically equivalent neutral species.

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43 66 A way towards advancing our understanding of food web dynamics relies on the evaluation of
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45 67 hypotheses under the macroscopic lens. First, the integration of multiple energetic pathways by
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47 68 predators, was shown to be a powerful mechanism to stabilize predator dynamic and the whole food
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50 69 web (Rooney *et al.* 2006; Rooney & McCann 2012). Second, the negative scaling of body size and
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52 70 population variance (*i.e.* variance mass allometry, VMA) predicts a smaller variance in large-sized
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55 71 species (Cohen *et al.* 2012). Assuming a size structured food web, and low efficiency of energy

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4 72 transference between trophic levels, a relatively lower population variance in predators with respect to
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7 73 preys is expected. Both mechanisms, the coupling of multiple energy channels and the negative scaling
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10 74 of variance with body size are not mutually exclusive and predict a systematic decrease in community
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12 75 fluctuations and colonization and extinction at higher trophic levels. A main limitation for the
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14 76 evaluation of these predictions in particular and the empirical analysis of fluctuations and persistence
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16 77 distribution in general, is the lack of appropriate information. A proper representation of both
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19 78 persistence times and fluctuations require data for multiple species during long time periods, typically
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21 79 several generations, which is seldom available, but plankton is the exception.

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23 80 The base of oceanic food webs is composed of microscopic unicellular producers (*e.g.* diatoms)
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26 81 which are consumed by a complex array of predators including unicellular protists (*e.g.* ciliates) and
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28 82 crustacean metazoans (*e.g.* copepods) (Segura *et al.* 2013). Plankton dynamics regulate the flux of
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31 83 matter and energy towards upper trophic levels that in turn support fisheries and the exchange of CO₂
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33 84 with the atmosphere. Empirical evidence suggests that planktonic predators integrate different energetic
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35 85 pathways (Rooney *et al.* 2008), show similarities in scaling relationships to terrestrial organisms
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38 86 (DeLong & Vasseur 2012; Hatton *et al.* 2015) and present a wide range of dispersal strategies. Here,
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40 87 using the western English Channel Station L4 data composed of fifteen years of weekly information
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43 88 (~800 weeks) on abundance and size of more than 250 planktonic species, we tested the validity of the
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45 89 following predictions of the Neutral theory: 1) the distribution of community fluctuations (CF) at
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47 90 different trophic levels conformed to a symmetric distribution, 2) community fluctuations variance
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49 91 decreased with trophic level, 3) the aggregated persistence times distribution (APT) follows a truncated
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52 92 power law distribution with scaling exponent between 1.5 and 2.0, and 4) the existence of a negative
53
54 93 relationship between CF and APT.

94 MATERIAL and METHODS

95 *Sampling and species counting*

96 Sampling for the planktonic community (phyto-, microzoo- and zooplankton) at Station L4 in
97 the western English Channel was conducted weekly from 1988 (Eloire *et al.* 2010; Widdicombe *et al.*
98 2010). However a gap in phytoplankton sampling between 1994 and 1995 meant that we started our
99 series analysis with data from 1995 to 2012 (~800 weeks). Species were grouped in three coarse
100 trophic groups i) primary producers, ii) consumers and iii) predators. Primary producers (diatoms and
101 dinoflagellates) and consumers (ciliates and heterotrophic dinoflagellates) were identified and
102 enumerated using settlement microscopy (Utermöhl, 1958) while predators (*i.e.* copepods) were
103 identified and counted using a dissecting microscope. For a detailed description of sampling and
104 counting methods we refer to (Widdicombe *et al.* 2010) for primary producers and consumers and
105 (Eloire *et al.* 2010) for predators. Diatoms and dinoflagellates are microbial producers ranging from 5
106 to 100 μm in spherical equivalent diameter (ESD), while ciliates and heterotrophic dinoflagellates are
107 mostly heterotrophic unicellular predators ranging from 20 to 200 μm ESD. It is worth to mention that
108 most of these organisms are mixotrophic. Copepods are multi-cellular crustaceans with complex life
109 cycles and size ranging from 200 to 1000 μm ESD. As copepods present several feeding modes
110 (Hansen *et al.* 1994) they can be classified in several trophic levels. For copepods, we performed the
111 analysis twice; i) using all recorded species and ii) using only those species known to be omnivorous
112 after excluding carnivorous and parasitic species which can present different dynamics (Eloire *et al.*
113 2010). From here onwards we will refer to the groups (*i.e.* diatoms, copepods) as functional groups.
114 Overall, we analyzed CF and APT of populations including a vast range of sizes, life history traits and
115 trophic groups.

116

117 *Data analysis*

118 Population fluctuations (r_s) were estimated for each species by dividing abundance (N_{t+1}) by
119 abundance in the preceding week (N_t) and taking the logarithm of the ratio as in (Segura *et al.* 2013):

$$121 \quad r_s = \log(N_{t+1}/N_t) \quad (\text{eq. 3})$$

122
123 Next, we aggregated the population fluctuations of all species belonging to the same functional group
124 into a single vector. These aggregated population fluctuations or community fluctuations (CF) were
125 fitted with a Laplace distribution (eq. 1) where the location (μ) and scale ($\Phi > 0$) were estimated with
126 the VGAM package (Yee 2010) in statistical software R (R Core Team 2013). We evaluated if the
127 distribution conformed to a Laplace by means of the Kolmogorov-Smirnov test. In order to evaluate
128 zero sum dynamics, we tested if zero was included in the 95% confidence interval of μ . We evaluated
129 symmetry around the median of the CF distribution with the Miao, Gel and Gastwirth (MGG) test
130 (Miao *et al.* 2006) as implemented in the package lawstat (Gastwirth *et al.* 2015).

131 In order to estimate persistence time, we interpolated linearly for each species the abundance
132 time series as some samplings were not performed exactly every seven days. For each species, we
133 estimated species persistence time as the number of weeks (Δt) the species was present ($N_t > 0$) after
134 being locally extinct ($N_{t+\Delta t} = 0$), where t refers to the time of the first positive record. Then, we pooled
135 together the persistence times for all species within a functional group and the aggregated data was
136 used to fit parameters from a power-law with exponential cut-off (Eq. 2). We used maximum likelihood
137 estimators as calculated in the R codes provided by <http://tuvalu.santafe.edu/~aaronc/powerlaws/>.
138 Characteristic timescale (τ) was defined as the inverse of the decay rate parameter ($\tau = 1/\nu$). We

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139 evaluated the power law distribution with exponential cut-off excluding the probability of observing a
140 persistence of 1 week.

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142 RESULTS

143 A total of 38695 abundances were recorded in the study period. Community fluctuations were
144 calculated for 253 species classified in five phylogenetic groups including 128 Diatoms, 38
145 Dinoflagellates, 30 Ciliates, 38 Heterotrophic Dinoflagellates and 35 Copepod species. They were
146 aggregated into three functional groups: primary producers, consumers and predators. CF in all
147 functional groups were long-tailed and visually conformed to a Laplace distribution (Fig. 1) although
148 formal tests rejected this hypothesis (K-S; $D > 2$; $p > 0.05$). Mean over all groups was not different from
149 zero (average (s.d.) = 0.001 (0.006)) and the distributions were symmetric around the median (MGG
150 test, $p > 0.05$) for all groups except for the heterotrophic dinoflagellates (MGG test, $p < 0.01$). As
151 expected in our working hypothesis, we found a consistent trend in community variability decreasing
152 from primary producers (Diatoms $\sigma_r^2 = 2.89$; Dinoflagellates $\sigma_r^2 = 2.57$), to consumers (Ciliates $\sigma_r^2 =$
153 1.78; Heterotrophic dinoflagellates $\sigma_r^2 = 1.45$), to predators (Copepods $\sigma_r^2 = 1.39$ and Omnivorous
154 copepods $\sigma_r^2 = 1.25$).

155 A power-law distribution with an exponential cut-off, Eq. 2, adequately described aggregated
156 persistence times (APT) for all functional groups (Fig. 2). The APT scaling exponent (α) systematically
157 increased across trophic levels and ranged from 0.58 to 1.19, values that are lower than predictions
158 based on neutral models (Bertuzzo *et al.* 2011). We found a strong negative correlation of the APT
159 scaling exponent (α) with the exponential decay rate (ν) (Pearson's $r = -0.98$; $P < 0.01$; $N = 6$).
160 Consequently, the shape of the persistence times distribution shifted from an exponential regime at
161 lower trophic levels towards a power law regime at higher trophic levels, and the characteristic
162 persistence time ($\tau = 1/\nu$) increased systematically from producers to predators (Fig. 3).

163 There was a strong correlation between community fluctuations variability (σ_r^2) and decay rate

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5 164 (v) (Pearson's $r = 0.92$, $p < 0.01$; $N = 6$). This implies that populations at lower trophic levels tend to be
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7 165 less persistent and more fluctuating than those at higher trophic levels (Fig. 3). Average group's body-
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9 166 size partially explained the difference in the variability and persistence between large-sized copepods
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11 167 and unicellular species. However, as predicted by our working hypothesis, trophic level alone also
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13 168 explained a significant fraction of the differences in fluctuations and persistence time distributions
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15 169 among similar-sized species (e.g. dinoflagellates, ciliates and heterotrophic dinoflagellates; Fig. 4).
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4 170 **DISCUSSION**

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6 171 We showed a consistent increase in community stability (decreased variability) and persistence times
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9 172 towards higher trophic levels in the species rich planktonic food web of the western English Channel.
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11 173 Three remarkable patterns were documented among trophic levels, i) the symmetry in populations
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13 174 fluctuations, ii) the decrease in variance of community fluctuations with body size and trophic level and
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15
16 175 iii) the systematic shift in the shape of the persistence times distribution with increasing trophic level.
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18 176 Consequently, the macroecological distributions herein analyzed provides a complementary support for
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20 177 current food web hypotheses (Hubbell 2001; Otto *et al.* 2007; Bertuzzo *et al.* 2011; McCann 2012).
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23 178 As expected, we found a systematic decrease in the variance of community fluctuations with
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25 179 body size and increasing trophic level (Cohen *et al.* 2012). Such patterns can be explained in terms of
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28 180 three main ecological principles: i) the Taylor law, which asserts that the variance of the population
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30 181 density of a set of populations is a power-law function of the mean population density (Taylor 1961), ii)
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32 182 the body size-density power law, according to which the mean population density of a set of
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35 183 populations is a negative power law of the organism body size (Peters & Wassenberg 1983; Kruk *et al.*
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37 184 2010) and iii) the fraction of energy lost at each trophic transference (Lindeman 1942) following the
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40 185 second law of thermodynamics. The former two were combined recently by Cohen *et al.*, (Cohen *et al.*
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42 186 2012) who coined the term variance-mass allometry (VMA) predicting a negative scaling of variance
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44 187 with body size within a single trophic level. Cohen *et al.*, (Cohen *et al.* 2012) stated that “if VMA [is]
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47 188 applied to marine or freshwater food webs, population densities of smaller-bodied species should be
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49 189 expected to be more variable spatially or temporally than population densities of larger bodied
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51 190 species”. Here we found that this trend hold, with larger copepods being less variable than small
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54 191 diatoms. Remarkably, the fluctuations and persistence for similar-sized species were determined by
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56 192 their trophic level as was observed for autotrophic and heterotrophic dinoflagellates or ciliates (Fig. 1
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& 2). This result expands the VMA for multiple trophic levels accounting for the fact that for similarly sized species, an increase in trophic level implies a decrease in average abundance (Widdicombe *et al.* 2010) and a reduction in the populations fluctuations and an increase in persistence. The progressive addition of energy channels with increasing body size represent a plausible mechanism to drive this pattern (Rooney *et al.* 2006; Arim *et al.* 2010; McCann 2012).

The negative relationship between persistence times of populations and community fluctuations supports previous predictions (Keitt & Stanley 1998; Pigolotti *et al.* 2005; Bertuzzo *et al.* 2011). It is intuitive that species with large fluctuations will face higher extinction risks, but the specific shape of the distribution of persistence times is also significant. Unexpectedly, we found that the shape of persistence time distribution varied systematically with trophic position (Fig. 3). The evidence of zero-sum dynamics at all levels together with the decrease of characteristic persistence timescale (τ ; Fig. 3) towards producers suggests that the recruitment and extinction rates are higher at the base and decreases towards the top of the food web as expected (Bertuzzo *et al.* 2011). However, the slope of the power law (α) was significantly shallower than expected by any of the predictions of the neutral model, irrespective of the structure of the spatial interaction network (Bertuzzo *et al.* 2011) This point to a profound effect of trophic dynamics in the shape of the persistence times distribution. Such changes in the shape of the distribution had not been described previously because analyses had been conducted either pooling occurrence data from trophically heterogeneous species (Keitt & Stanley 1998; Bertuzzo *et al.* 2011) or were based on single trophic level populations data from different systems (Suweis *et al.* 2012). It was suggested that the exponential term could be a statistical artifact caused by the short window of observation of the phenomenon (Keitt & Stanley 1998; Bertuzzo *et al.* 2011). Current results based on 200 (copepods) to 500 generations (primary producers) indicate otherwise. Also, the

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5 215 exponential term (v) decreased with trophic position where most persistent groups showed the
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7 216 minimum value. The systematic change in the persistence time distribution with trophic position
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10 217 deserves further scrutiny both in theoretical and empirical grounds.

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12 218 The prevalence of symmetric and long tailed distributions of population fluctuations across
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14 219 trophic levels and phylogenetic groups reported here points to a universal set of driving processes (Fig.
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16 220 1). These distributions further support the prevalence of balancing processes (*i.e.* zero-sum dynamics),
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19 221 in which a decline in one population is offset by an increase in other, at least at the large temporal scale
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21 222 of present observations (Hubbell 2001; Labra *et al.* 2008). This pattern is general within and among
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23 223 trophic levels and seems to be independent of species richness. Previous time series analyses
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26 224 determined that compensatory dynamics, a special case of balancing processes, were common in the
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28 225 plankton, but synchrony (*i.e.*, non-compensatory) was also recorded at specific scales of analyses
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31 226 (Vasseur & Gaedke 2007). The use of community fluctuations describe balancing processes without
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33 227 specifying the mechanisms (*e.g.* compensation, statistical averaging). However, community
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35 228 fluctuations represents a complete description of the concept of asynchrony in resource populations
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38 229 fluctuations (*e.g.* slow vs fast channels). The simplifying dichotomy of slow and fast channels
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40 230 involving asynchronous dynamics is expanded here to the whole food web, and evidenced by the
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42 231 observed compensatory dynamics, a prerequisite for food web stability (Rooney *et al.* 2006).

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45 232 Distributions of fluctuations failed a formal test of Laplace, a fact previously mentioned (Keitt
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47 233 & Stanley 1998) and recently evaluated (Kalyuzhny *et al.* 2014). In spite of formal test rejection, given
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50 234 the relatively good visual fit (Fig. 1) and parsimony principle, it is suggested to keep the Laplace
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52 235 distribution as a good statistical model to explore community fluctuations at large scales. A plausible
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54 236 explanation of the failure relies on the fact that Laplace is the result of mixing random iterates from
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237 normal distributions whose variances follow an exponential distribution (Kotz *et al.* 2001). If variances
238 of constituent distribution are not distributed exactly as an exponential distribution or constituent
239 distributions are fat tailed (Segura *et al.* 2013), a mixture between Gaussian and Lapace distribution is
240 expected as it seems to be the case here. In this sense, we caution the use of Central Limit Theorem to
241 anticipate a Gaussian distribution as the default null model. Indeed, the deviations from Gaussian
242 expectations can give insight into the driving ecological mechanisms. An exponential distribution of
243 variances of population fluctuations implies the existence of many populations with reduced variability
244 and a few populations with large fluctuations. This is congruent with the existence of fast and slow
245 energy channels in plankton dynamics (Rooney *et al.* 2006, 2008; McCann 2012). Populations within
246 the fast channel are expected to show large fluctuation in opposition to the expected dynamics on the
247 slow channel, with an overall strong role on the stabilization of food webs (Rooney & McCann 2012).

248 The empirical data should encompass the scale at which hypothetical mechanisms are expected
249 to operate (Levin 1992). The analysis of statistical distribution of populations' dynamics, represented in
250 fluctuations and persistence times, requires a large set of populations and a time span of several
251 generations (Keitt & Stanley 1998). The database of plankton in the western English Channel notably
252 fulfills these requirements. Congruently, clear distributions of populations' fluctuations and persistence
253 times were observed. Further, it was possible to relate the structure of these distributions with the body
254 size and trophic position of the functional groups considered. More importantly, the observed patterns
255 provide complementary support for sound theories previously analyzed with other approaches. That is
256 the case for the variance-mass scaling of Cohen *et al.*, (Cohen *et al.* 2012) and the stabilization of
257 populations and food web dynamics through the integration of asynchronous energy channels of
258 Rooney *et al.*, (Rooney *et al.* 2006). Further, novel trends are suggested as the change from an

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4 259 exponential to a power-law distribution of persistence time from basal to upper trophic positions which
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7 260 should be further explored. The framework provides explicit evaluation of community dynamics and
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9 261 brings novel explicit predictions by the integration of divergent hypotheses that should be evaluated
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12 262 theoretically and empirically.

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16 264 **Acknowledgment**

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For Review Only

FIGURES

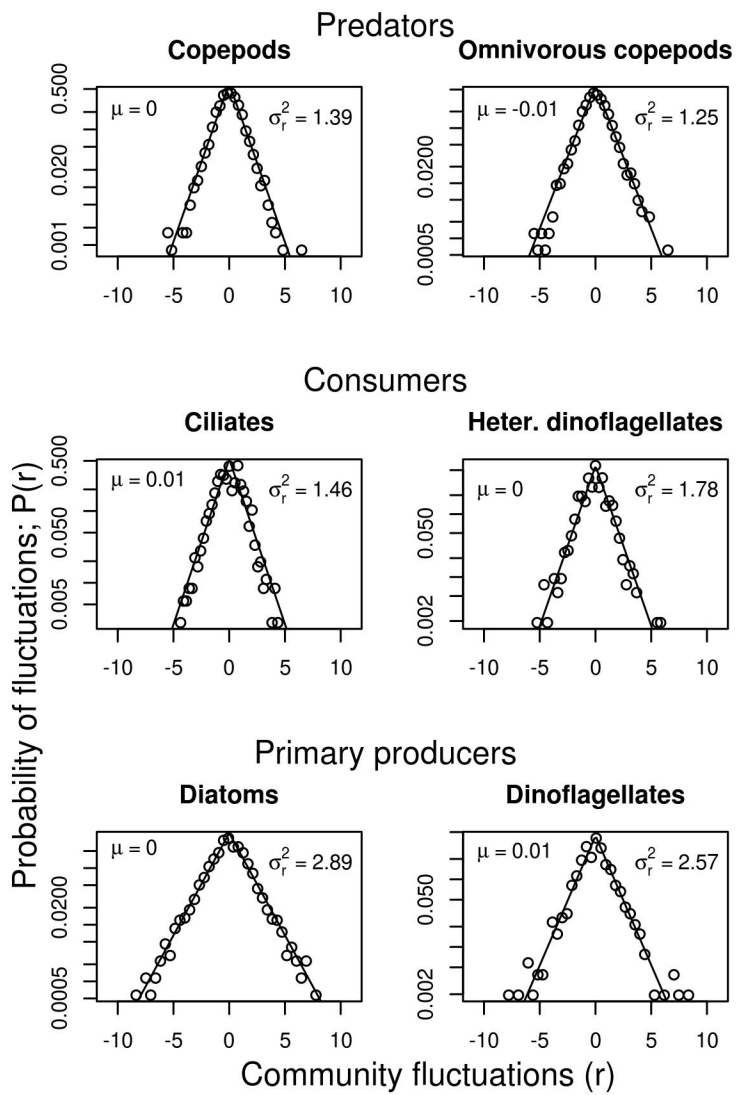


Figure 1.- Segura et al.

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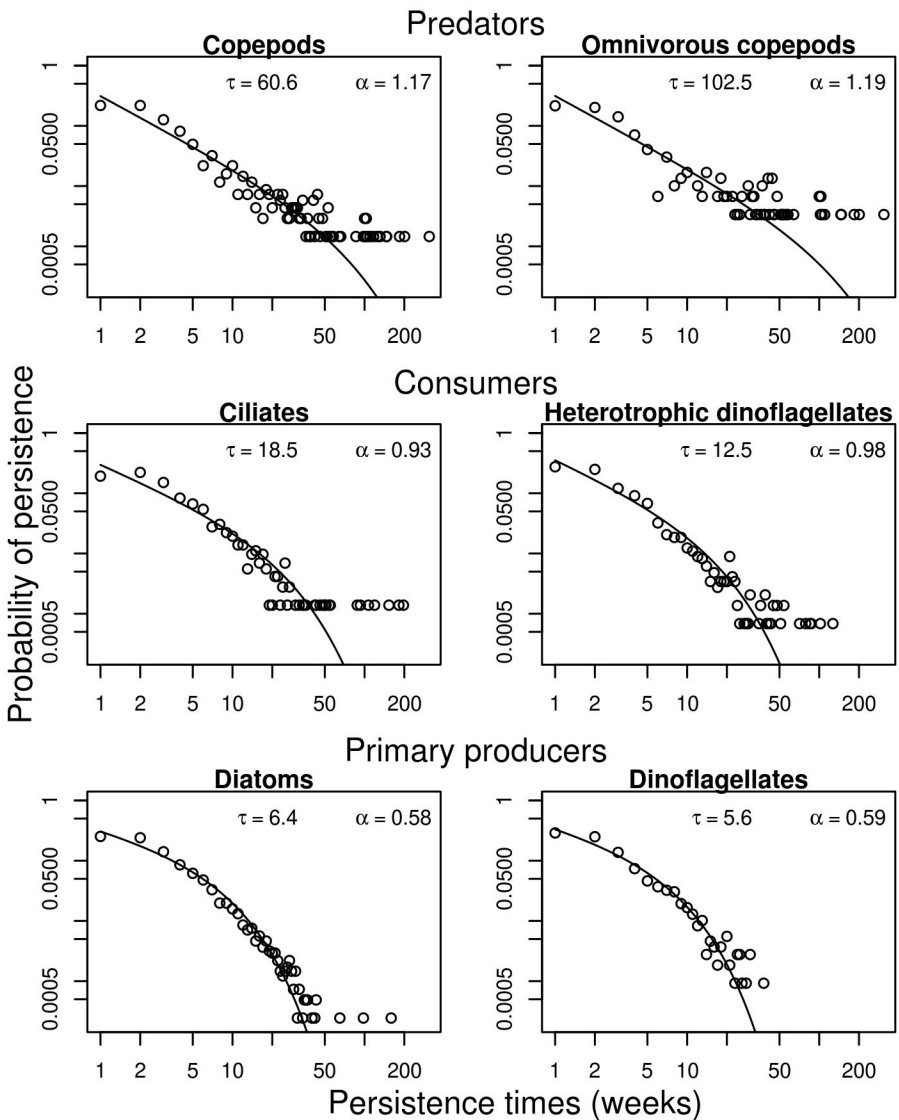
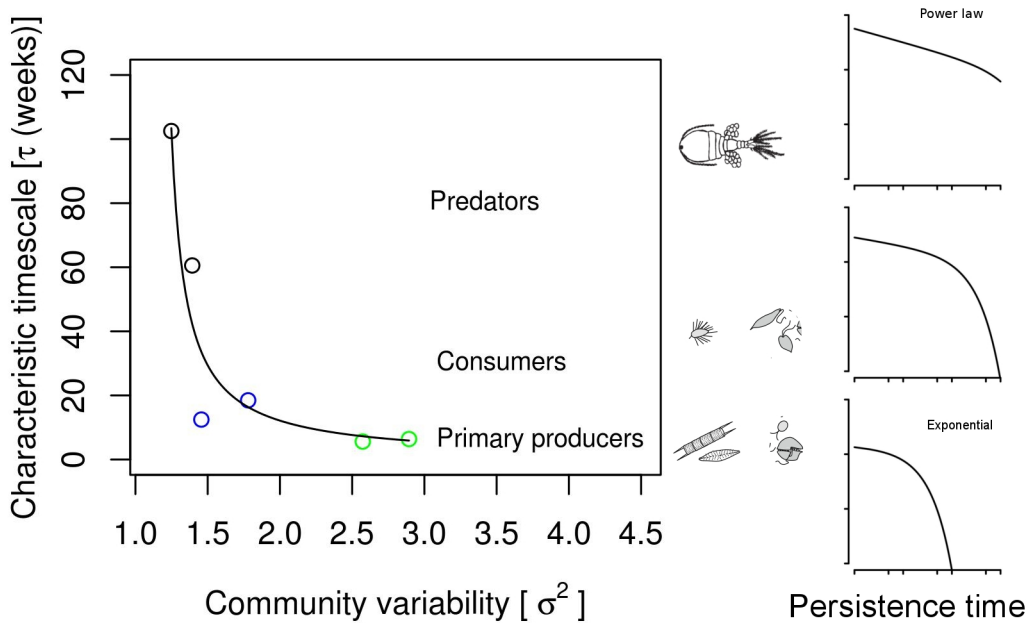


Figure 2.- Segura et al.,

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Figure 3.- Segura et al.

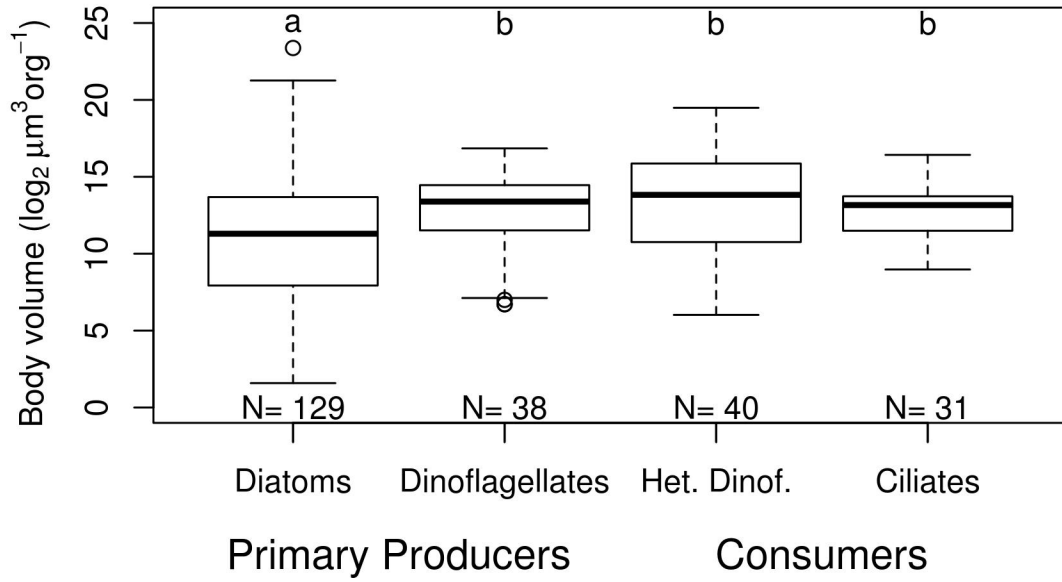


Figure 4.- Segura et al.

FIGURE LEGENDS

Figure 1.- Aggregated population fluctuations for each functional group at Station L4 in the western English Channel. Lines are the fitted models to original data and circles represent the middle point of the histogram and was generated for visual purposes only.

Figure 2.- Aggregated persistence time (APT) distribution for groups within each trophic level. The circles are the observed frequency distribution and the solid line is the fitted model ($P(t) = C t^{-\alpha} e^{-\nu t}$), where C is a normalization constant. Note the increase in the scaling exponent (α) and the characteristic timescale ($\tau = 1/\nu$) from producers to predators. Lines are the models fitted to original data and circles represent the middle point of the histogram and was generated for visual purposes only.

Figure 3.- Left, Negative relationship between variability and characteristic timescale times in the Station L4 planktonic food web. The solid line is the best fit least squares non-linear regression [$\tau = 10/(\sigma^2 - 1.14)$; $N=6$]. Right: schematic representation of the associated changes in the shape of the persistence times distribution among trophic levels.

Figure 4.- Body size distributions of producers and consumers in the English Channel L4 Station. Same letter “b” represents no differences among groups according to a log likelihood ratio test. Diatoms presented different size structure according to a log-likelihood ratio test ($p < 0.05$).