Spatiotemporal trends in zooplankton biomass in the northern Humboldt current system off Peru from 1961-2012

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Abstract :

Anchovy (*Engraulis ringens*) is the most important exploited fish species in the Northern Humboldt Current System (NHCS) off Peru. This species, as well as most other pelagic resources, mainly forage on zooplankton. The NHCS is bottom-up controlled at a variety of scales. Therefore, fish biomass is driven by the abundance of their prey. In this context, we studied the spatiotemporal patterns of zooplankton biomass in the NHCS from 1961-2012. Data were collected with Hensen net all along the Peruvian coast. To transform zooplankton biovolume into biomass we used a regression that was calibrated from 145 zooplankton samples collected during four surveys and, for which, precise information was available on both biovolume and wet weight. The regression model was then applied on a time-series encompassing 158 cruises performed by the Peruvian Institute of the Sea (IMARPE) between 1961 and 2012. We observed a clear multidecadal pattern and two regime shifts, in 1973 and 1992. Maximum biomass occurred between 1961 and 1973 (61.5 g m⁻²). The lowest biomass (17.8 g m⁻²) occurred between 1974 and 1992. Finally, the biomass increased after 1993 (26.6 g m⁻²) but without reaching the levels observed before 1973. A seasonal pattern was observed with significantly more biomass in spring than in other seasons. Spatially, zooplankton biomass was higher offshore and in northern and southern Peru. Interestingly, the zooplankton sampling was performed using classic zooplankton net that are well fitted to mesozooplankton and are known to underestimate the macrozooplankton; however, the spatiotemporal patterns we observed are consistent with those of macrozooplankton, in particular euphausiids. This suggests that in the NHCS, when and where macrozooplankton dominates it also dominates the biomass obtained using classic zooplankton net samples. Finally, until now, in the NHCS only time-series on zooplankton biovolume were available. The biomass data we provide are more directly usable in trophic or end-to-end models.

Keywords : Secondary production, Mesozooplankton, Macrozooplankton, Regime-shift, Spatiotemporal distribution, Decadal trends

1. Introduction

The Northern Humboldt Current System (NHCS) off Peru produces more fish per surface unit than any other marine ecosystem (Chavez et al., 2008). This system is characterised by an intense and shallow oxygen minimum zone (OMZ), which structures the ecosystem (Bertrand et al., 2011, 2014; Savattecí et al., 2019). The exceptional fish productivity observed since the early 20th century (Gutiérrez et al., 2009; Salvattecí et al., 2018, 2019) is maintained by the upwelling of cold, nutrient-rich, low-oxygen, subsurface waters, concentrating life in a thin surface layer (Bertrand et al., 2014). This system is also sustained by weaker winds than other upwelling systems due to the low latitude of the region and hence greater Coriolis factor per given amount of turbulence (Bakun and Weeks, 2008). The main fishery resource is the Peruvian anchovy (*Engraulis ringens*), which account for 65% of worldwide anchovy production (Eurofish, 2012) and supports more than 90% of the GDP (Gross Domestic Product) of the Peruvian fishery sector (INEI, 2013). Anchovy is central not only because it constitutes the backbone of Peruvian fishery exports, but also by the role it plays in the food chain (e.g. Espinoza and Bertrand, 2008). For a long time, it was thought that anchovy was foraging directly on phytoplankton and that such short food web was responsible for the high productivity of the system (Ryther, 1969; Walsh, 1981). However, recent studies demonstrated that anchovy, as well as other pelagic species such as sardine (*Sardinops sagax*), jack mackerel (*Trachurus murphyi*) and mackerel (*Scomber japonicus*), are mostly zooplanktivorous (Espinoza and Bertrand, 2008, 2014; Espinoza et al., 2009; Alegre et al., 2015).

As in many other pelagic upwelling systems (e.g. Lindegren et al., 2016), the NHCS is bottom-up controlled at a variety of spatiotemporal scales ranging from the internal-wave scale (minutes - 100 m–1 km) to millennial scales (Chavez et al., 2008;

Gutiérrez et al., 2009; Ayón et al., 2011; Bertrand et al., 2011, 2014; Salvatelli et al., 2014, 2019). Consequently, even if fish foraging can lead to local zooplankton depletion (Ayón et al., 2008b), changes in zooplankton biomass and composition directly impact higher trophic levels (Ayón et al., 2011; Bertrand et al., 2011; Alegre et al., 2015). Some studies already focused on the temporal trends in zooplankton biovolumes in the NHCS. Specifically, Ayón et al. (2004) and Ayón and Swartzman (2008) analysed the spatiotemporal trends in zooplankton biovolumes in the period 1964-2005 and identified four time regimes: high zooplankton biovolume prior to 1974.5, lower biovolume from 1974.5–1989.5, and average biovolume during 1989.5–1997.5 and 1997.5–2005. Each regime was also associated with different spatial and seasonal patterns of zooplankton biovolume.

To complete previous works, here we extend the series from Ayón et al. (2004) to the period 1961 – 2012 and express the zooplankton data in term of biomass instead of biovolume to be more directly applicable in energetic studies and trophic models. Also, we only use night data to better represent the total zooplankton biomass since most zooplankton diel migrate and take refuge within the OMZ at day (e.g. Ballón et al., 2011). With such data, we first examined decadal scales to identify possible regime shifts, but also studied the seasonal patterns to compare with previous studies. Second, we described the change in the spatial patterns of zooplankton distribution among decadal periods and seasons. Finally, previous published zooplankton time-series and this study are based on the use of classic zooplankton net (mesh size: 300 μm) that are fitted to observe mesozooplankton but are known to underestimate the macrozooplankton (e.g., Fleminger and Clutter, 1965). However, off Peru most pelagic fish take the bulk of their energy from macrozooplankton (Espinoza and Bertrand, 2008; Espinoza et al., 2009, Alegre et al.,

2015). We therefore discuss if the image of the zooplankton community we provide is consistent with macrozooplankton abundance.

2. Materials and Methods

Data were collected all along the diel cycle during 158 scientific surveys carried along the Peruvian coast by the Peruvian Institute of the Sea (IMARPE) between 1961 and 2012 (Fig. 1). Survey data covered the region up to 200 km from the coast but more than 95% of the data were collected within the first 100 km from the coastline. Zooplankton samples were collected by means of Hensen nets of 0.33 m² mouth area with 300 µm mesh, in vertical hauls from 50 m depth up to the surface. The zooplankton biovolume (ml) was determined immediately after collection using the displacement method (Frolander, 1954, 1957; Kramer et al., 1972). Ichthyoplankton, that can damage other zooplankton individuals, and large coelenterates (>2 cm), that could bias the conversion from biovolume to biomass, were removed before determining the biovolume (Postel et al., 2000; Ayón et al., 2004). Samples were then fixed with 2% formaldehyde buffered with borax.

Here, to estimate the total zooplankton biovolume and biomass we only considered the 7538 plankton samples collected during the night. Indeed, diel vertical migration is a major feature in zooplankton (e.g. Haury et al., 1978). Off Peru, most abundant zooplanktonic species perform diel vertical migration (Ayón et al., 2008a). Ballón et al. (2011) estimated that 79% of macrozooplankton biomass vertically migrate and take refuge in the oxygen minimum zone during the day (Bertrand et al., 2008, 2014, Ballón et al., 2011). Finally, pelagic fish are adapted to this pattern since they can fit their foraging period and duration to prey availability in the surface layer (Espinoza and Bertrand, 2008).

The biovolume (in ml) of each zooplankton sample was converted into total biovolume (in ml m⁻²) using the mouth area of the net (0.33 m²). To convert this total biovolume into wet weight biomass (in g m⁻²) we used the following equation (Wiebe et al., 1975; Wiebe, 1988):

$$\text{Log } (DV) = a \text{ WW} + b,$$

where *DV* is the displacement volume or biovolume (in ml m⁻²) and *WW* the wet weight (in g m⁻²), and *a* (slope) and *b* (intercept) are the coefficients of the regression. To estimate the terms of the equation we used a set of 145 zooplankton samples from four surveys performed in 1996 (46), 1998 (30), 2000 (34) and 2003 (35), for which we fully estimated both the displacement volume and the wet weight. These data encompass a large range of conditions (e.g. extreme El Niño in 1998 and strong La Niña in 2000) to ensure robustness. This equation was further applied to the entire set of data to convert biovolume onto wet weigh biomass.

The annual zooplankton biomass was estimated by averaging the different surveys performed in each year. To seek for significant shifts in zooplankton biomass between 1961 and 2012 we applied the Chow test (Chow, 1960).

To describe spatial variation among periods and seasons we interpolated the data with the “kriging” method using Surfer v.15.0. For spatial analysis, the Peruvian coast has also been divided into three latitudinal areas: A (03°30’S-05°59’S), B (06°00’S-13°59’S) and C (14°00’S-18°20’S) according to previous works on the spatial patterns of oceanographic conditions (e.g. Carrasco and Lozano, 1989), oxygen concentration (e.g. Bertrand et al., 2010), primary productivity (e.g. Echevin et al., 2008), zooplankton distribution (e.g. Ballón et al., 2011) and anchovy distribution (e.g. Simmonds et al., 2009).

The biomass were compared by period (resulting from the Chow test), by area (areas A, B and C), by season (Spring, Summer, Autumn and Winter) and according to the

ecological domain (Inshore, Offshore). Differences between factors were tested using an ANOVA. Before performing the analyses, we normalised the data by applying a Box-Cox transformation (Box and Cox, 1964).

3. Results

The a (slope) and b (intercept) terms of the biovolume-wet weight biomass equation were estimated to be 0.9896 and 0.016, respectively ($r^2 = 0.986$) (Fig. 2).

3.1. Spatiotemporal patterns at the decadal scale

Mean annual zooplankton biomasses varied between 3.7 g.m^{-2} and 100.6 g.m^{-2} . The lowest biomass was recorded in 1976 and the highest in 1967 (Fig. 3). Highest biomasses were found during the first years of our time series, these values progressively dropped in the early 1970s. Then, the biomass increased from the 1990s but without reaching the high values of the 1960s. Indeed, the Chow test depicted two significant regime shifts, in 1973 and 1992. Differences between periods were highly significant (ANOVA $p < 0.0001$). Maximum biomass occurred between 1961 and 1973 (mean 61.5 g.m^{-2}). The lowest biomass (17.8 g.m^{-2}) occurred during the second period between 1974 and 1992. Finally, the biomass was average (26.6 g.m^{-2}) during the third period that began in 1993 (Fig. 3, Table 1).

Spatially the zooplankton biomass presented different patterns according to the period (Fig. 4, Table 1). During the first period (1961-1973), the biomass was significantly higher

offshore than inshore (ANOVA, $p < 0.0001$). This pattern was not observed in the following periods that had similar biomass offshore and inshore.

The biomasses were significantly different between Areas (ANOVA, $p < 0.0001$), being significantly higher in the north (area A) in all periods (Fig. 4, Table 1). The lower biomass was observed in centre-north (area B), except during the last period when biomass was similar between areas B and C (southern Peru).

3.2. Spatiotemporal patterns at the seasonal scale

Zooplankton biomass presented a significant seasonal (ANOVA, $p < 0.0001$) pattern (Fig. 5) with a maximum in spring (48.3 g.m^{-2}), a minimum in autumn (25.5 g.m^{-2}) while summer and winter biomass were alike with 30.4 g.m^{-2} and 30.6 g.m^{-2} , respectively (Table 1). The seasonal differences were strongest during the first period than then after.

In spring, when the highest biomass occur, the bulk of zooplankton was distributed offshore (Table 2). This difference was much lower in autumn when the estimated biomass was the lower (Table 2). The biomasses were higher in Area A in summer and autumn, while in spring and winter they were similarly distributed among the three areas (Fig. 6, Table 2).

4. Discussion

The two significant regime shifts observed in 1973 and 1992 are slightly different from those proposed by Ayón and Swartzman (2008) (1974.5, 1989.5 and 1997.5). These differences can be related to at least two aspects. First, contrarily to this study, they used both day and night data, which can confound the results since most zooplankton undergo

diel vertical migration (Ballón et al., 2011). Second, our discrimination is based on biomass only when Ayón and Swartzman (2008) considered a variety of spatiotemporal factors including the diel cycle.

However, the shifts we depicted are consistent with the semi-qualitative analysis performed by Ayón et al. (2011) that studied the relative dominance of different size-classes of over 15,000 zooplankton data between 1963 and 2005. They showed that the temporal patterns of large zooplankton in general and euphausiids in particular, presented different periods, similar to those we observed considering the total biomass. They observed higher proportion of macrozooplankton before the mid-1970s and after the mid-1990s. Macrozooplankton avoid nets, in particular small nets, because of both visual and mechanical disturbances (Fleminger and Clutter, 1965; Debby et al., 2004; Lawson et al. 2008). The spatiotemporal patterns we observed are globally consistent with those of macrozooplankton, in particular euphausiids (Ayón et al., 2011; Ballón et al., 2011). Therefore, in the NHCS, when and where macrozooplankton dominates, it also dominates the biomass obtained using classic zooplankton net samples. This suggests that large organisms such as euphausiids and large copepods likely dominate the zooplankton biomass in the NHCS and govern our biomass time-series, but are underestimated by our sampling method. Ayón et al. (2011) showed that anchovy abundance was significantly correlated to macrozooplankton dominance, which is also partially represented in our time series. These results are also consistent with the fact that small pelagic fish forage on larger zooplankters in the NHCS when compared with other eastern boundary current systems (Espinoza et al., 2009).

Interestingly, anchovy, which forage on zooplankton, showed a significant shift in 1992 with an increase in abundance after this date that stabilised in the late 1990s (Gutiérrez et al., 2007). Alegre et al. (2015) also observed a shift in the diet composition of

the jack mackerel in the early 1990s. Similarly, a copepod biomass (1988-2008) from northern Chile (Escribano et al., 2012) also showed a similar shift in 1992. Escribano et al. (2012) observed, however, a strong decline in copepod biomass during and after the 1997-98 El Niño that we do not observe in our data. Finally, the regime shifts we observed are consistent with Bertrand et al. (2011) who showed that anchovy flourish under relatively low oxygen conditions that are also characterised by high macrozooplankton biomass. We conclude that a major re-structuring of the system occurred, therefore, in the early 1970s and 1990s.

While we observed significant decadal shifts, extreme El Niño (e.g. 1982-83 and 1997-98) or strong La Niña (e.g. 1975 or 2000) events did not appear to trigger these regime shifts. Similar observations were observed in a variety of ecosystem components with no evident effect (e.g. anchovy diet, Espinoza and Bertrand, 2008, or mackerel and jack mackerel diet, Alegre et al., 2015). As stated by Alegre et al. (2015), in this system, macrozooplankton abundance seem highly resilient to El Niño events (see also Brinton, 1967 and Arones et al., 2009).

Ballón et al. (2011) reviewed the zooplankton biomass estimations of meso- and macrozooplankton in two upwelling systems, Antarctic and eastern Canada. Estimates in upwelling systems ranged between 3.5 and 113.8 g m⁻² depending on the period or the system. For Peru, our estimates are higher than those from Ayón et al. (2004) converted into biomass by Ballón et al. (2011). This is likely due to the fact that we considered night samples only to provide a more robust estimation of the total biomass. Indeed, Ballón et al. (2011) estimated that ~79% of the macrozooplankton biomass perform diel migration and distribute in the deep layer during the day, out of range from the net sampling. Still, our estimations are far below the acoustic macrozooplankton biomass estimations from Ballón et al. (2011) (~100 g m⁻² during the mid-2000). Therefore, the total zooplankton biomass is

probably higher than our estimates but lower than the sum of our results and those of Ballón et al. (2011).

Our biomass results are comparable with the estimates in southern HCS off Chile (Escribano et al., 2009) and with measurements in the California, Canaria and Benguela Current systems for the period of the 1960s (Cushing, 1971). They are, however, much higher than recent estimates in the California Current system (e.g. Lavaniegos and Ohman, 2007).

Spatially we observed significantly more zooplankton biomass offshore than inshore during the first period (1961-1973). However, this trend was not observed in the two most recent periods. This result is puzzling since macrozooplankton biomass is much higher off the shelf break (Ballón et al., 2011). Indeed euphausiids are mainly distributed off the shelf where they use the oxygen minimum zone as a refuge area (Ballón et al., 2011). On the other hand, the consistent higher biomass observed in northern Peru (zone A) and lower biomass in central-north Peru (area B) is consistent with the results of Ballón et al. (2011). In all areas, we observed a decline in biomass during 1973-1992 but this reduction was stronger in the northern and southern areas.

Seasonally, we observed the highest zooplankton biomass in spring, rather low values in summer and winter and the lowest biomass in autumn, which is consistent with Ayón et al. (2008a). In northern Peru, Arones et al. (2009) observed higher zooplankton abundance in summer and autumn than spring. However, this study focused on a specific transect during a shorter period (1994-2004, with the exclusion of the El Niño-La Niña period ranging from Feb. 1997 to Nov. 1999). Overall our results are consistent with the fact that spring-summer are the periods of highest primary productivity in the NHCS (Echevin et al., 2008; Passuni et al., 2016, 2018) and when the oceanic front is closer to the coast (Swartzman et al., 2008), concentrating overall productivity.

In conclusion, this study provides the first estimation of zooplankton biomass in the NHCS off Peru over a multi-decadal period. We depicted two significant regime shifts in 1973 and 1992. The highest biomass occurred before 1973, the lowest during 1973-1992 and average values then after. These shifts are consistent with other studies on zooplankton or forage fish (e.g. Gutiérrez et al., 2007; Ayón et al., 2011). Spatially, zooplankton biomass was higher offshore and in northern and southern Peru. Zooplankton biomass was also higher during spring than other seasons. Finally, until now, only time-series on zooplankton biovolume were available for the NHCS (Carrasco and Lozano, 1989; Ayón et al., 2004; Ayón and Swartzman, 2008). The biomass data we provide here are more directly usable in trophic and end-to-end models.

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References

- Alegre, A., Bertrand, A., Espino, M., Espinoza, P., Dioses, T., Ñiquen, P., Navarro, I., Simier, M., Ménard, F., 2015. Diet diversity of jack and chub mackerels and ecosystem changes in the northern Humboldt Current system: a long-term study. *Prog. Oceanogr.* 137, 299-313.
- Aronés, K., Ayón, P., Hirche, H.J., Schwamborn, R. 2009. Hydrographic structure and zooplankton abundance and diversity off Paita, northern Peru (1994 to 2004)—ENSO effects, trends and changes. *J. Mar. Syst.*, 78, 582-598.
- Ayón P, Purca S, Guevara-Carrasco R., 2004. Zooplankton volume trends off Peru between 1964 and 2001. *ICES J. Mar. Sci. Symp.* 61:478–484.
- Ayón, P., G. Swartzman., 2008. Changes in the long-term distribution of zooplankton in the Humboldt Current Ecosystem off Peru, 1961–2005, and its relationship to regime shifts and environmental factors. *Fish. Oceanogr.* 17:6, 421-431.
- Ayón, P., Criales-Hernandez, M.I., Schwamborn, R., Hirche, H.J., 2008a. Zooplankton research off Peru: a review. *Prog. Oceanogr.* 79, 238–255.
- Ayón P., Swartzman G., Bertrand A., Gutiérrez M., Bertrand S. 2008b. Zooplankton and forage fish species off Peru: large-scale bottom-up forcing and local-scale depletion. *Prog. Oceanogr.*, 79: 208-214. DOI: 10.1016/j.pocean.2008.10.023
- Ayón, P., Swartzman, G., Espinoza, P., Bertrand, A., 2011. Long-term changes in zooplankton size distribution in the Peruvian Humboldt Current System: conditions favouring sardine or anchovy. *Mar. Ecol. Prog. Ser.* 422, 211-222.
- Ballón M, Bertrand A, Lebourges-Dhaussy A, Gutiérrez M, Ayón P, Grados D, Gerlotto F., 2011. Is there enough zooplankton to feed forage fish population off Peru? An

- 309 acoustic (positive) answer. Prog. Oceanogr. 91, 360-381.
 310 doi:10.1016/j.pocean.2011.03.001.
- 311 Bakun, A., & Weeks, S. J. 2008. The marine ecosystem off Peru: What are the secrets of
 312 its fishery productivity and what might its future hold?. Prog. Oceanogr. 79(2-4), 290-
 313 299.
- 314 Bertrand, A., Ballón, M., Chaigneau, A. 2010. Acoustic observation of living organisms
 315 reveals the oxygen minimum zone. PLoS ONE 5, e10330.
- 316 Bertrand, A., Gerlotto, F., Bertrand, S., Gutiérrez, M., Alza, L., Chipollini, A., Díaz, E.,
 317 Espinoza, P., Ledesma, J., Quesquén, R., Peraltilla, S., Chavez, F., 2008. Schooling
 318 behaviour and environmental forcing in relation to anchoveta distribution: an analysis
 319 across multiple spatial scales. Prog. Oceanogr. 79(2-4), 264-277.
- 320 Bertrand, A., Chaigneau, A., Peraltilla, S., Ledesma, J., Graco, M., Monetti, F., Chavez, F.,
 321 2011. Oxygen, a fundamental property regulating pelagic ecosystem structure in the
 322 coastal southeastern tropical Pacific. PLoS ONE 6, e29558.
- 323 Bertrand, A., Grados, D., Colas, F., Bertrand, S., Capet, X., Chaigneau, A., Vargas, G.,
 324 Mousseigne, A., Fablet, R., 2014. Broad impacts of fine-scale dynamics on seascape
 325 structure from zooplankton to seabirds. Nat. Com. 5, 5239.
- 326 Box, G.E.P., Cox, D. R. 1964. An analysis of transformations. J. R. Stat. Soc. Series B
 327 Stat. Methodol., 26, 211-234.
- 328 Brinton, E. 1967. Vertical migration and avoidance capability of euphausiids in the
 329 California Current. Lim. Oceanogr. 12(3), 451-483.
- 330 Carrasco, S., Lozano, O., 1989. Seasonal and long-term variations of zooplankton
 331 volumes in the Peruvian Sea 1964 - 1987. In The Peruvian Upwelling Ecosystem:
 332 Dynamics and Interactions, pp. 82-85. Ed. by D. Pauly, D. Muck, J. Mendo, and I.
 333 Tsukayama. ICLARM. 438pp.

- 334 Chavez, F.P., Bertrand, A., Guevara-Carrasco, R., Soler, P., Csirke, J., 2008. The northern
335 Humboldt Current System: brief history, present status and a view towards the future.
336 Prog. Oceanogr. 79, 95–105. DOI: [10.1016/j.pocean.2008.10.012](https://doi.org/10.1016/j.pocean.2008.10.012).
- 337 Chow, G.C., 1960. Tests of equality between sets of coefficients in two linear
338 regressions. Econometrica: J. Econ. Soc. 591-605.
- 339 Cushing, D.H., 1971. Upwelling and the production of fish. Adv. Mar. Biol. 9, 255–300.
- 340 Debby, L., Jackson, G.A., Angel, M.V., Lampitt, R.S., Burd, A.B., 2004. Effect of
341 netavoidance on estimates of diel vertical migration. Lim. Oceanogr. 46, 2297–2303.
- 342 Echevin, V., Aumont, O., Ledesma, J., Flores, G., 2008. The seasonal cycle of surface
343 chlorophyll in the Peruvian upwelling system: A modelling study. Prog.
344 Oceanogr. 79(2-4), 167-176.
- 345 Escribano, R., Hidalgo, P., Krautz, C., 2009. Zooplankton associated with the oxygen
346 minimum zone system in the northern upwelling region of Chile during March 2000.
347 Deep-Sea Res. Part II 56, 1083–1094.
- 348 Escribano, R., Hidalgo, P., Fuentes, M., Donoso, K., 2012. Zooplankton time series in the
349 coastal zone off Chile: Variation in upwelling and responses of the copepod
350 community. Prog. Oceanogr. 97, 174-186.
- 351 Espinoza, P., Bertrand, A., 2008. Revisiting Peruvian anchovy (*Engraulis ringens*)
352 trophodynamics provides a new vision of the Humboldt Current system. Prog.
353 Oceanogr. 79, 215–227.
- 354 Espinoza, P., Bertrand, A., 2014. Ontogenetic and spatiotemporal variability in anchoveta
355 *Engraulis ringens* diet off Peru. J. fish biol. 84(2), 422-435.
- 356 Espinoza, P., Bertrand, A., Van der Lingen, C.D., Garrido, S., Rojas de Mendiola, B.,
357 2009. Diet of sardine (*Sardinops sagax*) in the northern Humboldt Current system and

- 358 comparison with the diets of clupeoids in this and other eastern boundary upwelling
359 systems. Prog. Oceanogr. 83, 242–250.
- 360 Eurofish International Organisation., 2012. Overview of the world's anchovy sector and
361 trade possibilities for Georgian anchovy products Organisation, available at:
362 [http://www.fao.org/fileadmin/user_upload/Europe/documents/Publications/
363 Anchovies_report_2.03.2012.pdf](http://www.fao.org/fileadmin/user_upload/Europe/documents/Publications/Anchovies_report_2.03.2012.pdf).
- 364 Fleminger, A., Clutter, R.I., 1965. Avoidance of towed nets by zooplankton. Lim.
365 Oceanogr. 10, 96–104.
- 366 Frolander H., 1954. Plankton volume displacement indicator. University of Washington
367 Department of Oceanography. Seattle 5, WASHINGTON. Tech. Report N° 25.
- 368 Frolander, H. F. 1957. A plankton volume indicator. ICES J. Mar. Sci. 22(3), 278-283.
- 369 Gutierrez, M., Swartzman, G., Bertrand, A., Bertrand, S., 2007. Anchovy (*Engraulis*
370 *ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the
371 Humboldt Current ecosystem, Peru, from 1983–2003. Fish. Oceanogr. 16(2), 155-168.
- 372 Gutiérrez, D., Sifeddine, A., Field, D., Ortlieb, L., Vargas, G., Chavez, F. Velazco,
373 F., Ferreira, V., Tapia, P., Salvatelli, R., Boucher, H., Morales, M. C., Valdes, J., Reyss,
374 J.-L., Campusano, A., Boussafir, M. Mandeng-Yogo, M., Garcia, M. and Baumgartner,
375 T., 2009. Rapid reorganization in ocean biogeochemistry off Peru towards the end of
376 the Little Ice Age. Biogeoscience 6, 835-848.
- 377 Haury, L. R., McGowan, J. A., & Wiebe, P. H. 1978. Patterns and processes in the time-
378 space scales of plankton distributions. In *Spatial pattern in plankton communities* (pp.
379 277-327). Springer, Boston, MA.
- 380 INEI., 2013. Compendio Estadístico del Perú. Instituto Nacional de Estadística e
381 Informatica. www.inei.gob.pe.

- 382 Kramer, D., Kalin, M.J., Stevens, E.G., Thrailkill, J.R., and Zweifel, J.R., 1972. Collecting
383 and processing data on fish eggs and larvae in the California Current region. NOAA
384 Tech. Rep. NMFS Circ-370: 1-38.
- 385 Lavaniegos, B.E., Ohman, M.D., 2007. Coherence of long-term variations of zooplankton
386 in two sectors of the California Current system. *Prog. Oceanogr.* 75, 42–69.
- 387 Lawson, G. L., Wiebe, P. H., Ashjian, C. J., & Stanton, T. K., 2008. Euphausiid
388 distribution along the Western Antarctic Peninsula—Part B: distribution of euphausiid
389 aggregations and biomass, and associations with environmental features. *Deep-Sea Res.*
390 Part II 55(3-4), 432-454.
- 391 Lindegren, M., Checkley, D.M., Ohman, M.D., Koslow, J.A., Goericke R. 2016.
392 Resilience and stability of a pelagic marine ecosystem *Proc. R. Soc. B Biol. Sci.*, 283, p.
393 20151931.
- 394 Passuni, G., Barbraud, C., Chaigneau, A., Demarcq, H., Ledesma, J., Bertrand, A.,
395 Castillo, R., Perea, A., Mori, J., Viblanc, V.A., Torres-Maita, J., Bertrand, S., 2016.
396 Seasonality in marine ecosystems: Peruvian seabirds, anchovy and oceanographic
397 conditions. *Ecology* 97(1), 182-193. <https://doi.org/10.1890/14-1134.1>.
- 398 Passuni, G., Barbraud, C., Chaigneau, A., Bertrand, A., Oliveros-Ramos, R., Ledesma, J.,
399 Castillo, R., Bouchon, M., Bertrand, S., 2018. Long-term changes in the breeding
400 seasonality of Peruvian seabirds and regime shifts in the Northern Humboldt Current
401 System. *Mar. Ecol. Progr. Ser.* 597, 231-242.
- 402 Postel, L., Fock, H., & Hagen, W. 2000. Biomass and abundance. In *ICES zooplankton*
403 *methodology manual* (pp. 83-192). Academic Press.
- 404 Ryther J. H., 1969. Photosynthesis and fish production in the sea. *Sci.* 166: 72-76.
- 405 Salvatteci, R., Gutiérrez, D., Field, D., Sifeddine, A., Ortlieb, L., Bouloubassi, I.,
406 Boussafir, M., Boucher, H., Cetin, F., 2014. The response of the Peruvian Upwelling

Ecosystem to centennial-scale global change during the last two millennia. *Clim Past*. 10(2), 715-731.

Salvatteci, R., Gutierrez, D., Field, D., Sifeddine, A., Ortlieb, L., Caquineau, S., Baumgartner, T., Ferreira, V., Bertrand, A. 2019. Fish debris in sediments from the last 25 kyr in the Humboldt Current reveal the role of productivity and oxygen on small pelagic fishes. *Prog. Oceanogr.*, In Press. DOI: 10.1016/j.pocean.2019.05.006

Simmonds, J., Gutiérrez, M., Chipolini, A., Gerlotto, F., Woillez, M., Bertrand, A. 2009. Acoustic surveys for Peruvian anchoveta: Optimisation of survey design. *ICES J. Mar. Sci.*, 66, 1341-1348.

Swartzman, G., Bertrand, A., Gutiérrez, M., Bertrand, S., Vasquez, L. 2008. The relationship of anchovy and sardine to water masses in the Peruvian Humboldt Current System from 1983-2005. *Prog. Oceanogr.*, 79, 228-237.

Walsh, J. J., 1981. A carbon budget for overfishing off Peru. *Nature*, 290(5804), 300.

Wiebe, P.H., 1988. Functional regression equations for zooplankton displacement volume, wet weight, dry weight and carbon: a correction. *Fish. Bull.* 86,

Wiebe, P.H., Boyd, S.H., Cox, J.L., 1975. Relationships between zooplankton displacement volume, wet weight, dry weight, and carbon. *Fish. Bull. US* 73, 777–786.

1 TABLES

2

3 Table 1. Zooplankton mean biomass (in g m^{-2}) by season and by ecological domain for the
 4 complete time-series and by period.

Period	Total	Summer	Autumn	Winter	Spring	Inshore	Offshore	Area A	Area B	Area C
								A		C
1961-1973	61.5	62.4	35.2	42.0	92.1	42.3	70.4	93.7	49.7	76.6
1974-1992	17.8	17.9	19.0	15.2	19.7	17.1	18.2	23.1	16.6	17.9
1993-2012	26.6	25.8	23.7	25.7	30.2	19.8	30.7	35.7	25.6	24.0
All	34.6	30.4	25.5	30.6	48.3	24.8	40.0	47.0	31.0	36.1

5

6 Table 2. Zooplankton mean seasonal biomass (in g m^{-2}) by area and ecological domain.

Area	Summer		Autumn		Winter		Spring	
	Inshore	Offshore	Inshore	Offshore	Inshore	Offshore	Inshore	Offshore
A	26.7	57.2	21.8	36.2	22.7	44.5	50.6	74.0
B	20.0	36.6	21.2	26.7	27.6	29.2	30.0	48.3
C	13.5	25.7	17.5	26.0	25.8	32.3	41.1	61.4
All	20.2	36.7	20.9	28.0	27.2	32.3	32.2	56.6

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8 Figures

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12 Fig. 1. Study area and position of the 7538 zooplankton sampling points (black dots). The
13 red solid line depicts the shelf break position (isobaths of 200 m).

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Fig. 2. Log-linear relationships between zooplankton biovolume and wet weight.

Fig. 3. Box plot of zooplankton biomass (in g.m^{-2}) by year from 1961 – 2012. The size of the box is determined by the upper and lower quartiles, median is indicated as a horizontal line inside the box. The black dots represent the outliers. The Chow test depicted two significant shifts in 1973 and 1992 (vertical black lines).

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30 Fig. 4. Spatial distribution of zooplankton biomass (in g m^{-2}) by period. The horizontal
 31 blue dashed lines depict the limit of the three latitudinal areas. The black dots represent the
 32 sampling positions.

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Fig. 5. Boxplot of zooplankton biomass (in g m^{-2}) by season. The black dots represent the outliers.

Fig. 6. Spatial distribution of zooplankton biomass (in g m^{-2}) by season. The horizontal blue dashed lines depict the limit of the three latitudinal areas. The black dots represent the sampling positions.

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Dear Editor

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