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Seasonality of zooplankton active flux in subtropical waters

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Abstract

The biological carbon pump (BCP) is the mechanism by which the ocean transports organic matter below the mixed layer, exporting or sequestering it for years to millennia. Physical transport of dissolved and particulate organic carbon, the sinking of particles, and the carbon transported by diel and seasonal vertical migrants are the three main mechanisms of the BCP. In the study of active flux, seasonality is almost unknown and changes in ocean productivity during the annual cycle could promote differences in this transport. Here, we show the results of a cruise performed during spring in the Canary Current System, where we studied zooplankton active flux in two transects from the coastal zone off Northwest Africa toward the ocean. We measured biomass and the enzymatic activity of the electron transfer system (ETS) as a proxy for respiration in the water column down to a depth of 900 m. Compared with a previous survey during fall, we found higher values of specific ETS activity in the mesopelagic zone, promoting a higher active flux. Our results showed that the seasonality of active flux is driven not only by differences in biomass but also by differences in respiration rates in the mesopelagic zone, mainly due to differences in zooplankton body size. A review of the zooplankton active flux values around the Canary Islands showed a fourfold increase during spring compared with other seasons. This small window of higher flux should be considered in models of active carbon export in the ocean.

Knowledge of the functioning of the biological carbon pump (BCP) is of paramount importance for disentangling the role of the ocean in exporting (carbon entering the permanent thermocline) and sequestering carbon dioxide (carbon entering the thermohaline circulation, both sensu Lampitt et al. 2008). Quantification of this downward transport is also of importance for determining the capacity of the ocean to regulate climate change. A relatively small portion of the carbon entering the ocean is stored in the mesopelagic and bathypelagic layers for decades or centuries. Most of the carbon is released into the atmosphere again due to respiration after its circulation through the different biological pathways (del Giorgio and Duarte 2002).

Three main mechanisms promote the downward carbon transport: (1) the so-called gravitational flux due to the sinking of particulate organic carbon (POC) and its remineralization below the mixed layer, (2) the physical transport of POC and dissolved organic carbon (DOC) produced by biological activity in the epipelagic zone, and (3) active transport due to the diel and seasonal vertical migration of zooplankton and micronekton (migrant pump). These organisms feed in the upper layers of the ocean and migrate toward the mesopelagic and bathypelagic layers to avoid visual predation. There, they respire, excrete, and egest carbon, in addition to being predated at depth. By far, most of the research on the BCP was related to the gravitational flux as a main mechanism of downward carbon transport. Nowicki et al. (2022) found that this transport was responsible for 70% of the total global carbon export, while physical mixing was responsible for 20%, and the migrant pump for the remaining 10%.

Published values of active transport are quite variable in relation to the POC flux. Active flux was only 4–6% of

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Additional Supporting Information may be found in the online version of this article.

Author Contribution Statement: SHL designed the active flux study, was responsible for the data acquisition, and wrote the first draft. JML and EF compiled and processed the data for both cruises. ASL, LA, IMS, AL, ASDL, and JDP ensured the quality of the data, performed the data analysis, made the figures, and prepared its publication in Pangaea. MC and VT performed the GAM model. All authors contributed to interpretation and writing, revised the manuscript, and approved the final version.

the POC flux in the central and western equatorial Pacific (Le Borgne and Rodier 1997), while values over 100% of the POC flux were observed by Hernández-León et al. (2019*a*) considering the transport performed by both zooplankton and micronekton. Interestingly, the latter authors found a rather high variability of active flux related to primary production in the tropical and subtropical Atlantic Ocean.

However, the data availability regarding active flux in the ocean is still quite limited, and there is a considerable lack of data on different ocean provinces (Longhurst 2006). The variability in zooplankton active flux in relation to areas of different productivity was studied by Hernández-León et al. (2019*a*) at a basin scale from the very oligotrophic waters off Brazil to the oceanic upwelling system off Northwest Africa. They found that most of the downward flux was driven by the sinking of particles in the oligotrophic zones, while in areas of higher productivity, the flux was mostly performed by zooplankton and micronekton. This higher flux driven by the pelagic fauna was also found by Stukel et al. (2018) in the rather productive area of the Costa Rica Dome. Thus, as expected, the variability of active flux is related to the productivity level. Higher values of primary production promote higher values of zooplankton and micronekton active flux. Therefore, as most of the ocean is oligotrophic, low values of active flux are expected at the global scale (Aumont et al. 2018; Archibald et al. 2019; Nowicki et al. 2022). However, as observed in coastal upwelling zones, areas of high productivity could show much higher values of passive than active flux. Stukel et al. (2023) showed rather high active flux but also higher gravitational flux. These systems are dominated by large diatoms with high sinking rates. Oceanic upwelling, as observed by Hernández-León et al. (2019*a*), showed a high proportion of small phytoplankton and a low proportion of diatoms (Armengol et al. 2019). Here, the high zooplankton biomass (feeding upon large phytoplankton and microplankton), as well as advection, could promote a passive flux that is lower than expected.

However, the seasonality of active flux is almost unknown. As this flux is related to primary production in the ocean (Hernández-León et al. 2019*a*), the variability in active flux is also expected to be related to differences in productivity among seasons. In particular, the euphotic zone of subtropical waters is nutrient enriched during winter due to convective mixing, promoting the so-called late winter bloom (LWB; Menzel and Ryther 1961). The increase in nutrients in the euphotic zone (De León and Braun 1973; Cianca et al. 2007) and the increase in productivity (De León and Braun 1973; Neuer et al. 2007) are propagated toward zooplankton (Hernández-León et al. 1984) and potentially to deep waters (Putzeys et al. 2011). Thus, an increase in productivity in the upper layers promotes a downward transport of carbon due to vertical migration. This increase in productivity seemed to promote an increased downward transport of carbon, as observed from the large zooplankton biomass at the mesopelagic and bathypelagic layers found below the productive layers at a global scale (Hernández-León et al. 2020).

Seasonality is poorly known, as estimates of zooplankton active flux are scarce. Hernández-León et al. (2019*b*) provided zooplankton active flux values in the Canary Current System (CCS) during the most oligotrophic (highly stratified) period in fall. They found low values of zooplankton active flux, as expected from the low primary production during this season. However, Putzeys et al. (2011) found an increase in zooplankton migrant biomass and active flux after the LWB in the Canary Island waters. They suggested that the phytoplankton and zooplankton bloom in the epipelagic zone is propagated to the mesopelagic zone, something that was also found by Hernández-León et al. (2020) regarding zooplankton biomass at the global scale.

During spring 2003, we had the opportunity to estimate active flux in the same area and oceanographic stations that were sampled by Hernández-León et al. (2019*b*), sailing from the upwelling zone off Northwest Africa to the low productive oceanic zone. Here, we show the results of zooplankton active flux measurements during spring just after the productive period in the CCS. Therefore, we will compare the zooplankton active flux values observed during the productive season (spring, present study) with those observed during the most oligotrophic season (fall, Hernández-León et al. 2019*b*) in the subtropical waters of the CCS. We will also compare both periods (spring and fall) in areas of different productivity (upwelling and oceanic zones).

Materials and methods

We studied the carbon flux in the CCS during the "Carbon flux at the Canary Atlantic Region" cruise (COCA II cruise). Sampling took place from May 20, 2003 to June 10, 2003, on board the R.V. "Hespérides." Two transects were performed: one transect was sampled south of the Canary Islands from the upwelling zone off Northwest Africa toward the ocean (Fig. 1; 26°N to 21°W). The other transect was sampled from the upwelling zone off Cape Blanc from 21°N to 26°W, covering the area where the Canary Current recirculates toward the west, including the Cape Verde Frontal Zone (CVFZ; Zenk et al. 1991), a thermohaline front showing the presence of the South Atlantic Central Water (SACW). In the text, we will refer to these transects as the northern transect (26°N) and the southern transect (21°N). Vertical profiles of temperature, conductivity, and depth were recorded in the 0–1000 m water column using a CTD Seabird 911plus mounted on a General Oceanics Rosette sampler equipped with 24 Niskin bottles (10 liters). The temperature anomaly (°C) between both seasons (fall minus spring) in the northern and southern transects were estimated from the CTD files averaged every 1dbar, and the interpolated values were added using the *ggplot2*

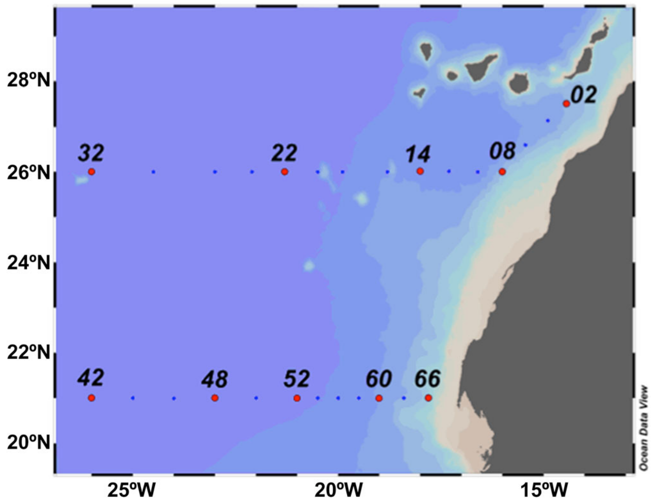

Fig. 1. Location of oceanographic stations during spring and fall showing the northern (Stas. 02–32) and southern (Stas. 42–66) transects. Red dots indicate stations sampled during day and nighttime used to estimate zooplankton active flux. Blue dots are stations sampled using a rosette and CTD.

(Wickham 2016) and *metR* (Campitelli 2021) packages in R (V.4.3.2) (R Core Team 2023).

Zooplankton biomass was sampled using a Longhurst-Hardy Plankton Recorder (LHPR; Longhurst and Williams 1976) net equipped with 200-μm net mesh on the way down from the surface to a depth of 900 m in oblique hauls at 2–4 knots. The volume filtered by the net varied between 2.6 and 50.0 m^3 (average 7.9 ± 4.05 m^3) per sample. Profiles of zooplankton biomass were performed around midday and at midnight in nine stations in order to account for the diel vertical migration of zooplankton. Sta. 32 was not sampled due to weather conditions. About 40 samples were obtained per haul, and for each sample we obtained the average depth between the minimum and the maximum depth provided by the depth sensor of the LHPR net. Samples were later averaged every 25 m in order to compare day and night hauls. In the laboratory on board, samples were collected from the cod-end of the net and split using the Motoda device (Motoda 1959). One of the subsamples was immediately frozen in liquid nitrogen (−196°C) for enzymatic activity measurements. The other one was preserved in 4% buffered formaldehyde for taxonomy and abundance measurements. Micronekton organisms, such as small mesopelagic fish or decapods captured by the net, were excluded from the samples.

Biomass was estimated by measuring the protein content of zooplankton. We homogenized the sample in a potter at 4°C, and a subsample was analyzed using the method of Lowry et al. (1951) modified by Rutter (1967) and using bovine serum albumin (BSA) as the standard. Protein content was converted to dry matter using the dry weight/protein ratio of 2.49 obtained by Hernández-León et al. (2019*c*). Hernández-León et al. (2019*b*) used a different ratio for the fall (COCA I) cruise, but to compare the results with those of the spring season (this study), we used the abovementioned ratio for both cruises. Dry matter was then converted to carbon assuming that 40% of the dry matter was carbon (Dam and Peterson 1993).

We used the enzymatic measurement of the electron transfer system (ETS) activity as a proxy for metabolism to estimate the respiratory flux of zooplankton. For this, another subsample of the homogenate was incubated at 18°C following the method of Packard (1971). Details of the procedure can be obtained elsewhere (e.g., Hernández-León and Gómez 1996). The specific ETS activity (in a biomass unit basis) was recalculated for the in situ temperature using the equation of Arrhenius using 15 kcal mol^{-1} as the activation energy (Packard et al. 1975).

The migrant biomass was obtained as the difference between the integrated values of day and night zooplankton biomass in the upper 200 m layer (Longhurst and Williams 1976) and converted to carbon units as shown above. The vertical distribution of the biomass showed higher values during the night in the upper layers because of the effect of the diel vertical migration (DVM), except in Sta. 02, where zooplankton biomass was higher during the day, and in Sta. 08, where biomass values were quite similar during the day and night. This counterintuitive result is due to the significant patchiness normally observed in upwelling zones and coastal transition zones in the epipelagic layer because of the high mesoscale variability in these zones (eddies, filaments, …). A difference of 12 h between day and night sampling in the same station (geographic position) could promote such a result. In these two stations, we estimated migrant biomass as the difference between day and night biomass in the mesopelagic zone (200–800 m layer). This is not a common procedure as organisms at depth could avoid the net during daytime (discussed in Hernández-León et al. 2001), and the migrant biomass assessed in this way is often an underestimation.

The respiratory flux was obtained from the average values of the specific ETS activity (μL O_2 mg $protein^{-1}$ h^{-1}) in the 200–800 m layer. This value was converted to respiration rates using a conservative respiration/ETS ratio of 0.5 (Hernández-León and Gómez 1996), 12 h of zooplankton residence at depth, and a respiratory quotient of 0.97 (Omori and Ikeda 1984). This respiration at depth was then multiplied by the migrant biomass in order to assess the respiratory flux of zooplankton diel vertical migrants in mg C m^{-2} 12 h^{-1}. Total active flux was also estimated considering respiration, excretion, and mortality at depth. Growth was estimated from respiration using the equation of Ikeda and Motoda (1978) assuming gross growth (growth/ingestion) and assimilation efficiencies of 30% and 70%, respectively, and growth was assumed to be equal to mortality in steady-state conditions. Dissolved organic excretion (DOC) by zooplankton was assumed to make up 24% of the respired plus excreted carbon (Steinberg et al. 2000). This value is probably higher as recently observed by Maas et al. (2021), but we used the previous value to compare our results with those of recent studies on active flux in the CCS. Similarly, active gut flux was not considered in our previous studies (Hernández-León et al. 2019*a*,*b*), so we do not include this parameter in our assessment of active flux for the sake of comparison. However, recent studies suggest that migrant copepods are able to promote gut flux (Tarrant et al. 2021). Thus, our assessment of the total active flux by zooplankton is quite conservative because of the use of conservative parameters, such as the respiration/ETS ratio, DOC excretion, and gut flux.

We also measured the abundance of zooplankton-like particles using a laboratory Optical Plankton Counter (OPC, Model OPC-1L, Focal Technologies Inc., Canada). The zooplankton sample from the LHPR net passed through a light beam of 2 cm × 4 mm (path length 2.5 cm), and the OPC provided a digital size unit (DSU) proportional to the light blocked by the particle (organism). The OPC could provide the equivalent spherical diameter (ESD) or equivalent circular diameter (ECD) of the particle, which is proportional to the DSU. The OPC-1L (normal setting) is effective in measuring ECDs in the range of 0.25–16 mm. However, for this study, we used only the number of particles in order to obtain a rough estimate of the body weight of the organisms by dividing the protein biomass of samples by the number of particles (organisms) detected by the OPC. As metabolism is closely related to the size of organisms, this body weight assessment provided information about the effects of body size in mesopelagic organisms and their differences among seasons.

Passive flux values and net primary production values were obtained from Arístegui et al. (2020). In that study, primary production was obtained from the Ocean Productivity website (http://www.science.oregonstate.edu/ocean.productivity/index.php) based on remote sensing data following Behrenfeld and Falkowski (1997) and using the vertical generalized production model (VGPM).

Differences in biomass, specific ETS activity, and body weight were assessed using a one-way ANOVA. The critical *p*-value of the ANOVA is given in the text to indicate the level of significance. Generalized additive models (GAMs) were applied to model the relationship between the response variables and the predictors. Prior to model fitting, ambient variables (temperature, salinity, and water density) were tested for collinearity using Spearman's correlation analysis (Kitchens and Rooker 2014). When high correlations ($|r| > 0.7$; Dormann et al. 2013) between any two variables existed, one of the variables was excluded to minimize collinearity (Zuur et al. 2009). In addition, variance inflation factors (VIFs) were calculated in the statistical program R, with VIF values above

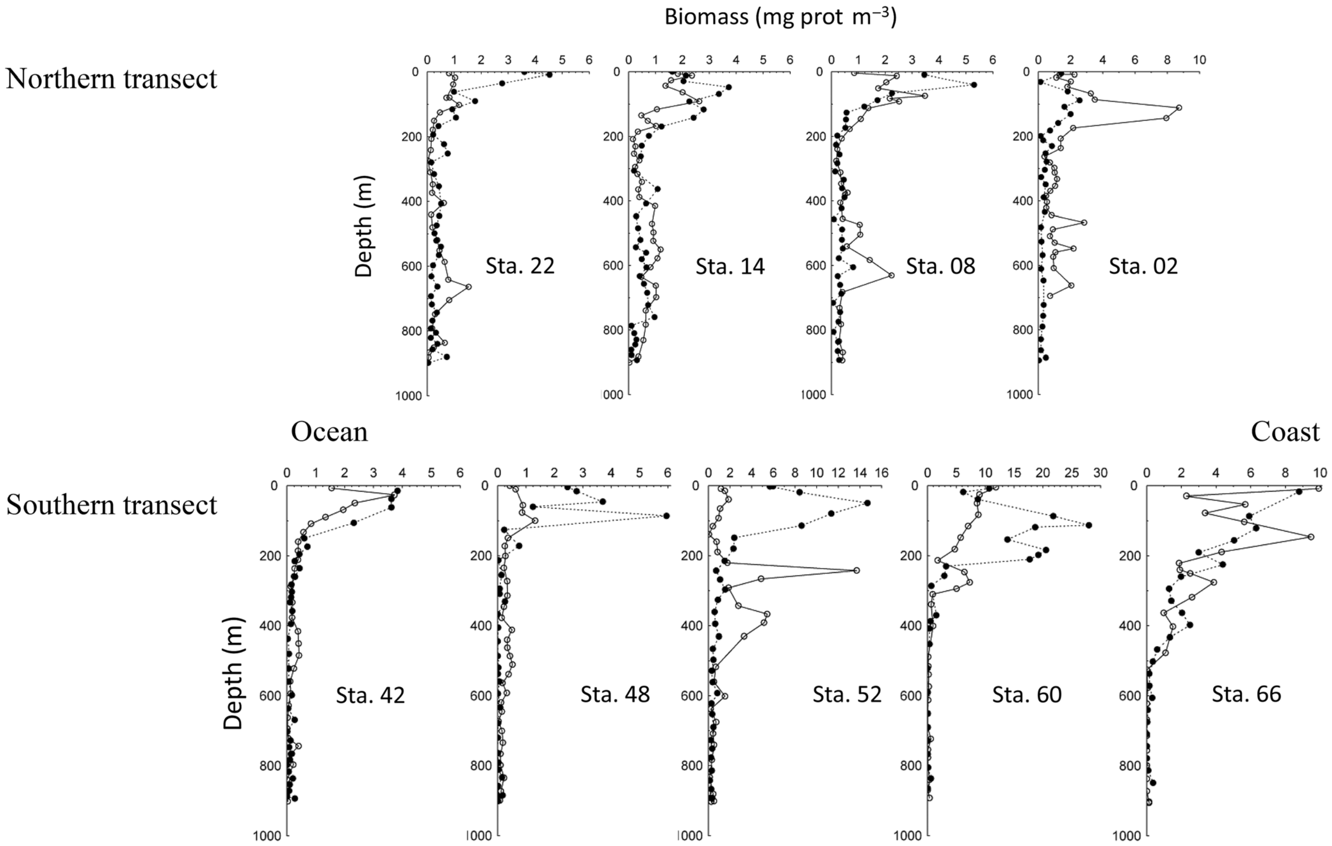

Fig. 2. Day (empty dots) and nighttime (black dots) values of zooplankton biomass for the northern (above) and southern (below) transects during the COCA II cruise in spring. Observe the different scale values in the *X*-axis.

Table 1. Specific electron transfer system (ETS) activity, respiration rates obtained in the 200–800 m depth interval, migrant biomass, respiratory flux, and total active flux obtained from respiratory flux (*see* "Materials and Methods" section) during spring and fall. Values are compared with the particulate organic carbon (POC) flux obtained using sediment traps. "dm" stands for dry matter.

	Station	Sp ETS activity (μL O$_2$ mg prot^{-1} h^{-1})	± SD	Respiration (μL O$_2$ mg prot^{-1} h^{-1})	Respiration (μL O$_2$ mg dm^{-1} h^{-1})	Respiration (d^{-1})	Migrant biomass (mg C m^{-2})	Respiratory flux (mg C m^{-2} 12 h^{-1})	Active flux (mg C m^{-2} 12 h^{-1})	Primary production (mg C m^{-2} d^{-1})	POC flux (mg C m^{-2} d^{-1})	RF/POC flux (%)	Active/ passive (%)
Spring	2	25.20	11.36	12.60	5.05	0.16	130.8	10.3	20.1	1046.3	—	—	—
	8	13.34	9.56	6.67	2.68	0.08	223.1	9.3	18.1	496.4	15.6	59.6	116.3
	14	22.68	7.63	11.34	4.55	0.14	206.5	14.6	28.6	431.0	8.4	174.3	340.0
	22	15.91	13.84	7.96	3.19	0.10	187.0	9.3	18.1	284.6	13.3	69.8	136.2
	Average				**3.87**	**0.12**	**186.8**	**10.9**	**21.2**	**564.6**	**12.4**	**101.3**	**197.5**
	± SD				1.12	0.03	40.2	2.5	5.0	333.1	3.7	63.5	123.8
	66	27.75	7.35	13.88	5.57	0.17	122.8	10.7	20.8	3680.2	73.2	14.6	28.4
	60	20.15	9.92	10.08	4.04	0.13	1751.4	110.3	215.2	3994.7	117.6	93.8	183.0
	52	12.45	6.72	6.23	2.50	0.08	1357.7	52.8	103.1	665.4	44.4	119.0	232.1
	48	18.03	12.23	9.02	3.62	0.11	272.6	15.4	30.0	497.2	13.3	115.4	225.0
	42	17.23	11.15	8.62	3.46	0.11	134.3	7.2	14.1	334.2	22.8	31.7	61.9
	Average				**3.84**	**0.12**	**727.8**	**39.3**	**76.6**	**1834.3**	**54.3**	**74.9**	**146.1**
	± SD				1.12	0.03	769.7	43.7	85.3	1835.7	42.2	48.6	94.8
Fall	2	6.36	4.82	3.18	1.27	0.04	281.8	5.6	10.92	1191.9	199.2	2.8	5.5
	8	4.83	2.75	2.42	0.97	0.03	156.1	2.4	4.60	496.0	58.8	4.0	7.8
	14	5.23	3.11	2.62	1.05	0.03	221.5	3.6	7.07	398.2	44.4	8.2	15.9
	22	6.73	4.51	3.37	1.35	0.04	46.4	1.0	1.91	268.5	28.8	3.4	6.6
	32	10.62	5.96	5.31	2.13	0.07	77.9	2.6	5.04	226.7	31.2	8.3	16.2
	Average				**1.35**	**0.04**	**156.7**	**3.0**	**5.91**	**516.2**	**72.48**	**5.3**	**10.4**
	± SD				0.46	0.01	97.8	1.7	3.35	392.4	71.84	2.7	5.2
	66	8.40	5.20	4.20	1.68	0.05	2258.9	59.3	115.64	9215.1	67.2	88.3	172.1
	60	4.51	3.28	2.26	0.90	0.03	285.1	4.0	7.84	5650.5	31.2	12.9	25.1
	52	11.28	6.99	5.64	2.26	0.07	198.5	7.0	13.65	677.7	9.6	72.9	142.1
	48	4.30	4.02	2.15	0.86	0.03	720.8	9.7	18.89	637.1	27.6	35.1	68.5
	42	16.42	17.02	8.21	3.29	0.10	34.8	1.8	3.49	390.2	8.4	21.3	41.5
	Average				**1.80**	**0.06**	**699.6**	**16.4**	**31.90**	**3314.1**	**28.80**	**46.1**	**89.9**
	± SD				1.02	0.03	907.8	24.2	47.17	3967.0	23.80	32.9	64.2

Note: Values in bold are average values for the above oceanographic stations.

3 being an indication of strong collinearity (Zuur et al. 2009). Additional information about the GAM is given in the Supporting Information.

Results

Zooplankton biomass and ETS activity during spring

The hydrographic section exhibited lower temperature values in the epipelagic zone during the spring cruise than during the fall cruise, as expected (Hernández-León et al. 2019*b*; Arístegui et al. 2020). Burgoa et al. (2020) made a complete description of water masses in the area during both the spring and the fall cruise. Most of the seasonal variability was observed in the southern boundary, in the Cape Verde Frontal Zone (CVFZ). Chlorophyll *a* (Chl *a*) was always higher in the southern transect, but it was also remarkably higher during spring than during fall in the whole area. This was expected because of the observed lower temperature values during spring in the upper layers.

Zooplankton biomass was higher in the stations affected by upwelling (Fig. 2), especially in the southern transect, where the presence of oceanic upwelling off Cape Blanc promoted higher values in the upper 500 m layer (Stas. 02, 60, and 66 were affected by upwelling). Sta. 52 was affected by the CVFZ (Burgoa et al. 2020) and showed higher zooplankton biomass. Migrant biomass was higher in the southern transect than in the northern transect during spring and fall, and the lowest values were observed in the most oceanic stations (Stas. 42 and 48; Table 1).

Specific ETS activity decreased with depth, as expected from the lower temperature in the mesopelagic zone (Fig. 3). However, values of ETS activity during day- and nighttime in the mesopelagic zone (the 200–800 m layer) were rather high, thereby promoting higher values of zooplankton respiration in the mesopelagic zone than during fall (Table 2). Estimates of respiration rates in the mesopelagic zone in both transects were rather similar in terms of dry matter (3.87 ± 1.12 and $3.84 \pm 1.12\ \mu\text{L O}_2\ \text{mg dm}^{-1}\ \text{h}^{-1}$), promoting specific respiration values of $0.12\ \text{d}^{-1}$ at depth (Table 1). These high respiration rates during spring also promoted high values of respiratory flux, even though the values of migrant biomass were in the range observed in previous studies in the area (Table 2). During spring, active flux, comprising respiratory, excretion, and mortality flux, was higher than passive flux in

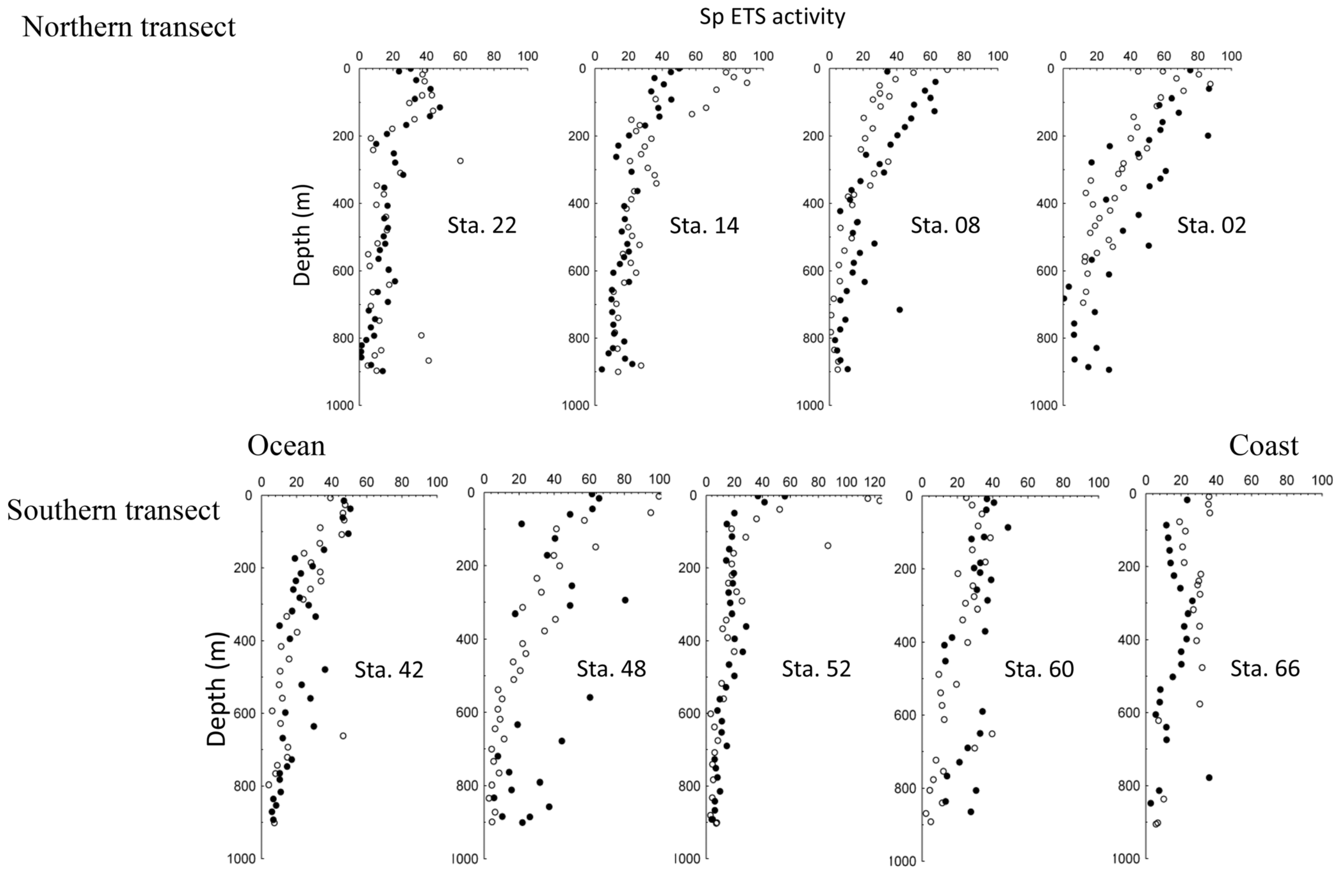

Fig. 3. Day (empty dots) and nighttime (black dots) values of zooplankton ETS activity (μL O_2 mg protein^{-1} h^{-1}) for the northern (above) and southern (below) transects during the COCA II cruise in spring.

Table 2. Comparison of respiration rates, migrant biomass, respiratory flux, total active flux, and particulate organic carbon (POC) flux during fall and spring seasons in northern and southern transects as well as in upwelling and oceanic stations. "dm" stands for dry matter.

		Respiration (μL O_2 mg dm^{-1} h^{-1})	Respiration (d^{-1})	Migrant biomass (mg C m^{-2})	Respiratory flux (mg C m^{-2} 12 h^{-1})	Active flux (mg C m^{-2} 12 h^{-1})	Primary production (mg C m^{-2} d^{-1})	POC flux (mg C m^{-2} d^{-1})	RF/ POC flux (%)	Active/ passive (%)
Spring	Northern	**3.87**	**0.12**	**186.8**	**10.9**	**21.2**	**564.6**	**12.4**	**101.3**	**197.5**
	Transect	1.12	0.03	40.2	2.5	5.0	333.1	3.7	63.5	123.8
	Southern	**3.84**	**0.12**	**727.8**	**39.3**	**76.6**	**1834.3**	**54.3**	**74.9**	**146.1**
	Transect	1.12	0.03	769.7	43.7	85.3	1835.7	42.2	48.6	94.8
	Both	**3.43**	**0.11**	**487.4**	**26.7**	**52.0**	**1270.0**	**38.6**	**84.8**	**165.3**
	Transects	1.34	0.04	614.9	34.4	67.1	1474.6	38.6	51.8	101.1
	Upwelling	**4.89**	**0.15**	**668.3**	**43.8**	**85.3**	**2907.0**	**95.4**	**54.2**	**105.7**
	Stations	0.78	0.024	938.0	57.7	112.4	1619.1	31.4	56.1	109.3
	Oceanic	**3.33**	**0.10**	**396.9**	**18.1**	**35.3**	**451.5**	**19.6**	**95.0**	**185.2**
	Stations	0.74	0.023	472.9	17.3	33.8	135.6	13.0	51.3	100.1
Fall	Northern	**0.65**	**0.02**	**156.7**	**3.0**	**5.9**	**516.24**	**72.5**	**5.3**	**10.4**
	Transect	0.22	0.01	97.8	1.7	3.3	392.43	71.8	2.7	5.2
	Southern	**0.86**	**0.03**	**699.6**	**16.4**	**31.9**	**3314.1**	**28.8**	**46.1**	**89.9**
	Transect	0.49	0.02	907.8	24.2	47.2	3967.0	23.8	32.9	64.2
	Both	**0.76**	**0.02**	**428.2**	**9.7**	**18.9**	**1915.2**	**50.6**	**25.7**	**50.1**
	Transects	0.37	0.01	672.6	17.6	34.4	3039.3	55.5	30.8	60.0
	Upwelling	**0.62**	**0.02**	**941.9**	**23.0**	**44.8**	**5352.5**	**99.2**	**34.7**	**67.6**
	Stations	0.19	0.01	1140.5	31.5	61.4	4019.9	88.5	46.7	91.1
	Oceanic	**0.81**	**0.03**	**208.0**	**4.0**	**7.8**	**442.0**	**29.8**	**21.9**	**42.7**
	Stations	0.43	0.01	237.7	3.2	6.2	172.0	17.9	25.2	49.1

Note: Values in bold are average values for the above oceanographic stations.

most of the stations (Table 1), showing average values of 197.5% ± 123.8% and 146.1% ± 94.8% for the northern and southern transects, respectively. This pattern was also found for the oceanic (185.2% ± 100.1%) and upwelling stations (105.7% ± 109.3%) (Table 2).

Comparison between spring and fall

The average values of biomass obtained in this study were compared with the average values obtained by Hernández-León et al. (2019*b*) during fall. We observed higher zooplankton biomass values in the mesopelagic zone during fall in

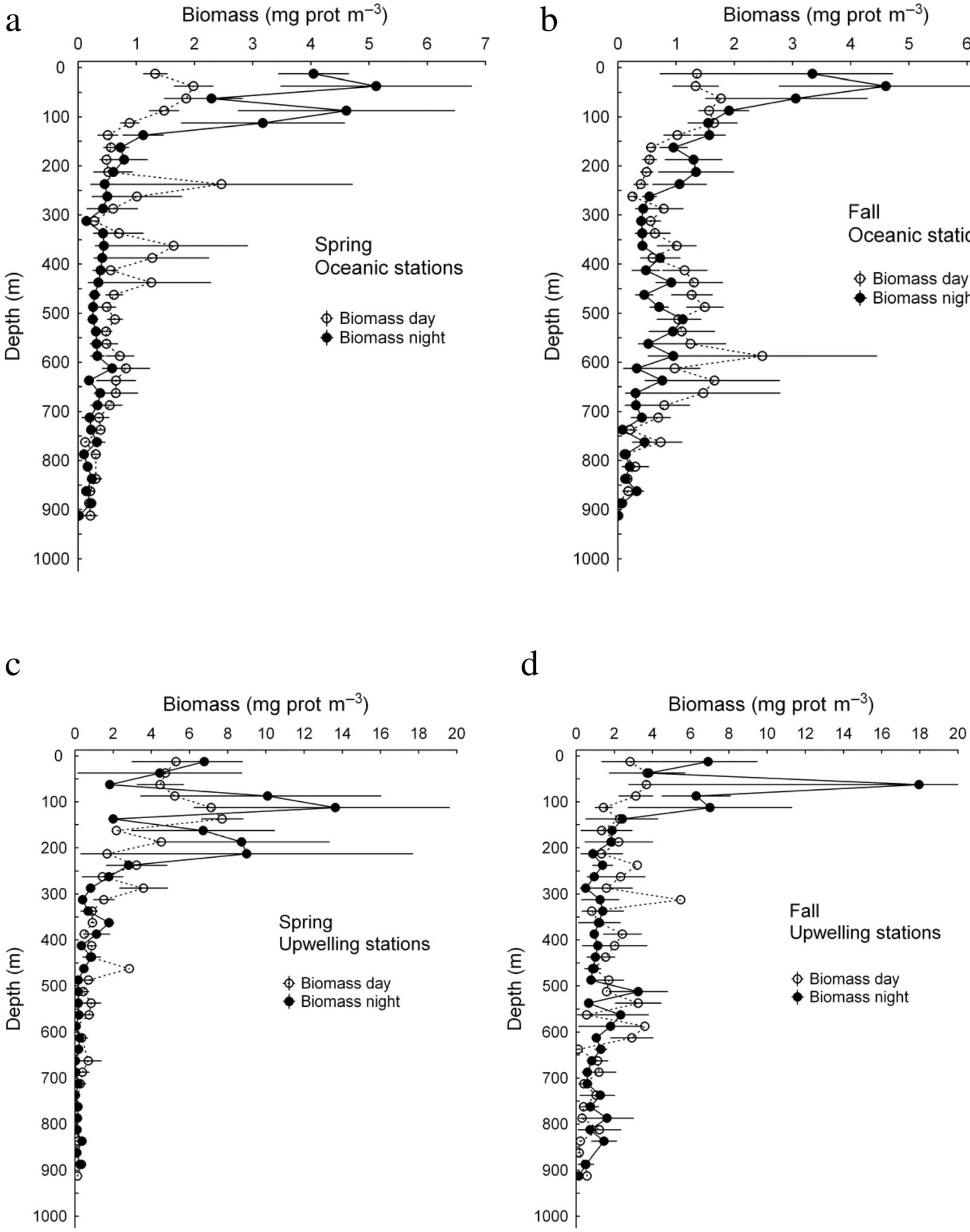

Fig. 4. Comparison of average values of biomass (± standard error) during fall and spring in oceanic and upwelling stations. Observe the different scale for biomass between oceanic (**a**, **b**) and upwelling (**c**, **d**) stations.

both oceanic and upwelling stations ($p < 0.05$, one-way ANOVA; Fig. 4; Supporting Information Fig. S1). Similarly, we found sharp differences in the vertical distribution of specific ETS activity between our study during spring and Hernández-León et al. (2019*b*) during fall. We observed higher values in our study (spring) compared with fall in the northern and southern transects as well as in the oceanic and upwelling stations (Fig. 5). These significantly ($p < 0.01$, one-way ANOVA) higher values were observed in the upper mesopelagic layer at a depth from about 200 to 500 m, except in the upwelling station, which reached a depth of 700 m. Below these depths, specific ETS activity was quite similar during both seasons.

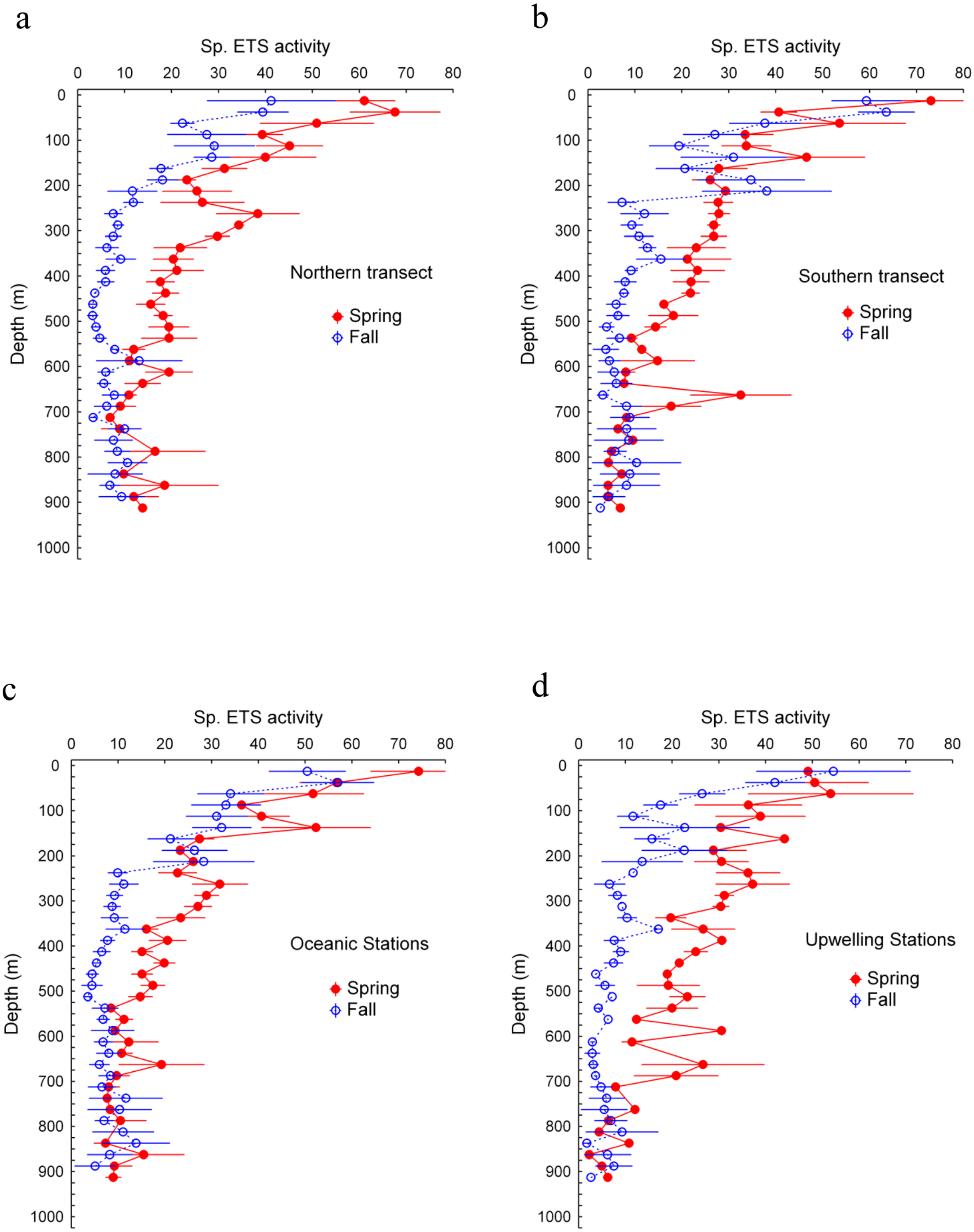

Fig. 5. Average values of specific electron transfer system (ETS) activity (μL O_2 mg protein^{-1} h^{-1} ± standard error) during spring (red dots) and fall (blue dots) in northern (**a**) and southern (**b**) transects as well as in oceanic (**c**) and upwelling (**d**) stations.

This higher ETS activity explains the higher active flux during spring despite the similar migrant biomass found during both seasons (Table 2). Comparing migrant biomass and respiratory flux, we found much higher values during spring than during fall (Supporting Information Fig. S2a). Migrant biomass and respiratory flux were significantly correlated with net primary

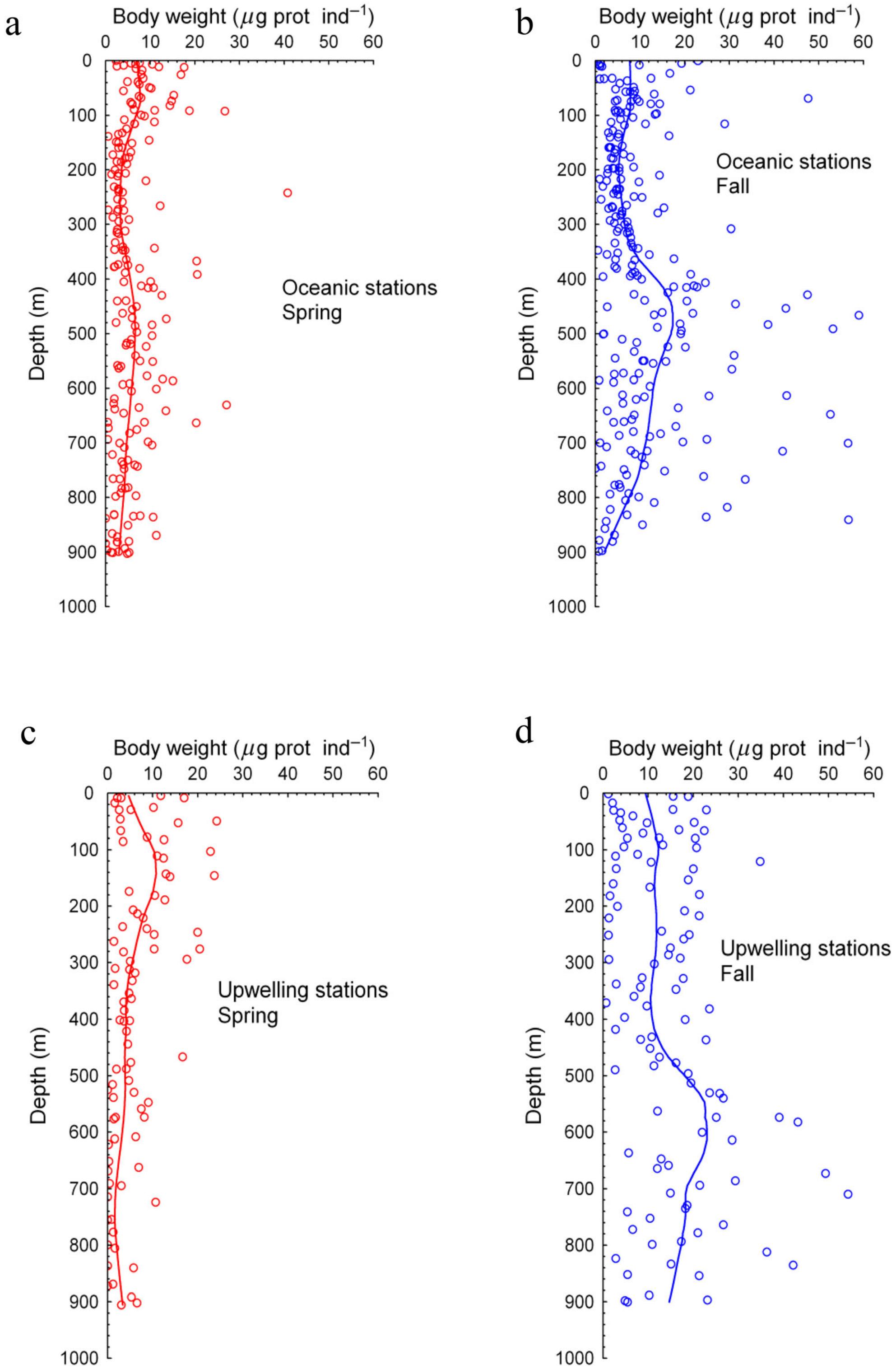

Fig. 6. Comparison of body weight during spring (red dots) and fall (blue dots), also comparing oceanic (**a**, **b**) and upwelling (**c**, **d**) stations. The red or blue line is the locally estimated scatterplot smoothing (LOESS spline).

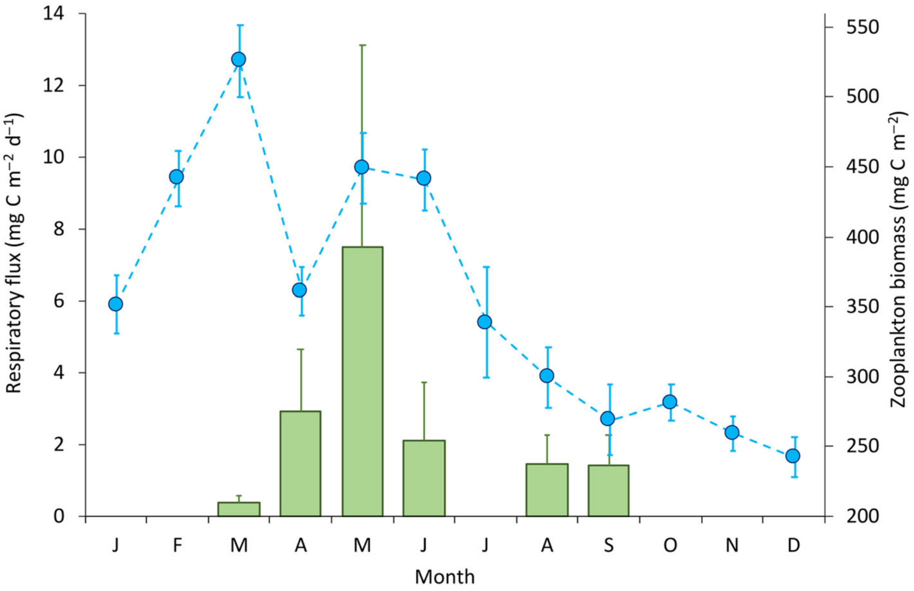

Fig. 7. Review of respiratory flux values obtained by different authors around the Canary Islands (green bars). Observe the fourfold increase during May compared to the stratified season (June, August, September). The zooplankton biomass (blue dots) is the 50-yr average value obtained by Couret et al. (2023) for the Canary Islands (*see* the text). Bars are standard error.

production obtained from remote sensing ($p < 0.001$ and $p < 0.01$, respectively), but with a low coefficient of determination ($r^2 = 0.395$ and $r^2 = 0.257$, Pearson correlation; Supporting Information Fig. S2b,c).

The temperature in the mesopelagic zone was rather similar during both spring and fall cruises, as indicated by the temperature anomaly between both seasons in the northern transect (Supporting Information Fig. S3a) and the southern transect (Supporting Information Fig. S3b). Thus, the sharp differences in specific ETS activity found between spring and fall in the mesopelagic zone were not promoted by temperature. We also observed the influence of mesoscale activity in the epipelagic layers, which was rather high south of the Canary Archipelago due to eddies shed by the islands, and at the southern section due to the interaction with the CVFZ (Hernández-León et al. 2019*b*; Arístegui et al. 2020). This mesoscale activity scarcely affected the temperature in the mesopelagic layer.

However, the body weight estimated from abundance and biomass showed clear differences among seasons. We found smaller organisms in the whole water column during spring than during fall (Fig. 6). This lower body weight during the spring season was observed in both upwelling and oceanic stations and coincided with differences in specific ETS activity between both seasons. We obtained significant differences ($p < 0.001$) between seasons in the oceanic stations (Fig. 6a,b) and between oceanic and upwelling stations (Fig. 6a,c) during spring ($p < 0.05$) and fall ($p < 0.001$) (Fig. 6b,d).

The abundance response plots resulting from the GAM (Supporting Information Fig. S5) were similar to the biomass responses for temperature and depth. There were higher abundances in spring and in the southern transect. The GAM results for specific ETS values (Supporting Information Fig. S6) showed that season greatly influenced specific ETS activities, with higher values during spring and higher values in the southern transect. The body weight response plots (Supporting Information Fig. S7) showed, as expected, lower body weight at higher temperatures and a sharp difference between seasons.

Seasonality of active flux

We reviewed the available zooplankton respiratory flux values around the Canary Islands for different sampling years from 1993 to 2015 to look for seasonal variability in the CCS. We found 7 studies and 25 values of respiratory flux (Supporting Information Table S2). We observed a fourfold increase during May (Fig. 7) just after the late winter bloom around the Canary Islands. Couret et al. (2023) showed an increase in epipelagic zooplankton biomass during March–April (average values over 50 yr) before the increase in respiratory flux during spring (Fig. 7). Although the data are biased by the interannual variability, this result suggests a clear seasonality of active flux due to the seasonal epipelagic zooplankton enrichment during late winter and the beginning of spring, which is transferred in part to the mesopelagic zone.

Discussion

Zooplankton active flux observed during two distinct seasons (spring and fall) in the CCS showed stark differences in the downward carbon transport performed by zooplankton migrants during the DVM. The differences in active flux between both seasons were also in accordance with the different productivity values found in the upper layers. The increase in primary production observed during the late winter bloom and early spring in the euphotic zone of subtropical waters (Hernández-León et al. 2007; Couret et al. 2023) is mirrored in the mesopelagic zone by an increment in specific metabolism of zooplankton. The sharp increase in specific ETS activity promoted an increase in zooplankton respiratory flux, even though the values of migrant biomass were rather similar between both seasons (Table 2). Another interesting observation was the increase in zooplankton biomass in the mesopelagic zone during fall (Fig. 4) during both daytime and nighttime.

Our spring and fall data were obtained early this century after the warming observed during the mid-1990s. This temperature increase coincided with a sharp change in the Atlantic Multi-decadal Oscillation (AMO), which denoted a drastic change in the physical properties of the North Atlantic Ocean (Alheit et al. 2014, 2019). This change in the temperature conditions, as reflected in the AMO, was also observed in the Canary Current by Arístegui et al. (2009). However, after this change, the AMO remained high, thus not indicating a cooling of the area. Therefore, our data provide information about a temperature regime that started during the last decade of the 20th century.

Seasonality in the mesopelagic zone

Studies on seasonality in the vertical distribution of zooplankton in the ocean are scarce, mainly due to the inherent difficulties of sampling the twilight zone. Among these studies, Andersen et al. (2001) showed a transition from the spring bloom to oligotrophy in the NW Mediterranean waters, pointing out the migration of several species and the downward seasonal migration of *Calanus helgolandicus*. They found a transfer of biomass after the bloom linked to ontogenetic migration. Koppelmann and Weikert (2007) also studied the vertical distribution of zooplankton in the Mediterranean Sea, showing the temporal evolution of abundance and biomass in the epipelagic, mesopelagic, and bathypelagic zones. They observed a clear increase in zooplankton in the mesopelagic and bathypelagic zones after a bloom in the shallower layers. The increase in zooplankton biomass in the mesopelagic zone after the late winter bloom in these subtropical waters was first observed by Hernández-León et al. (1984). They found a progressive downward increase in biomass during the months after the late winter bloom, suggesting a downward transport of energy and matter toward the mesopelagic zone. At a global scale, Hernández-León et al. (2020) observed a higher zooplankton biomass in the mesopelagic and bathypelagic zones in areas of higher primary production, also suggesting a downward transport of carbon to deep waters. Recently, Garcia-Herrera et al. (2022) studied the seasonality of zooplankton abundance and biomass in the mesopelagic layer of a Chilean Patagonian fjord, showing decreasing biomass values from the productive period (spring and summer) through autumn and winter. Our study clearly showed this increase in biomass (*see* ANOVA results) and abundance in the mesopelagic zone after the productive period in these subtropical waters. The magnitude of the mesopelagic zooplankton biomass depended on the productivity in the upper layers (Hernández-León et al. 2020), as observed here between the northern (less productive) and southern transects and between the oceanic (oligotrophic) and upwelling stations (Fig. 4).

However, migrant biomass was rather similar among seasons (Table 2), and the difference was related to the biomass during the night in the mesopelagic zone. Zooplankton biomass at night between a depth of 400 and 700 m varied during spring and fall (Fig. 4). During spring, the biomass values were lower in this layer, whereas during fall, they were significantly higher, denoting an increase in zooplankton biomass by night at this depth (Fig. 4). This is in accordance with a transfer of energy and matter to the mesopelagic zone after the productive period in these waters. In any case, migrant biomass varied depending on the productivity of the area. Migrant biomass was higher in the most productive areas, such as the upwelling zone, compared with the oceanic stations (Table 2). Putzeys et al. (2011) observed an increase in zooplankton migrant biomass after the late winter bloom in the Canary Island waters. They found a decrease in Chl *a* after the winter bloom parallel to a decrease in epipelagic zooplankton biomass but followed by an increase in zooplankton migrant biomass. They suggested a transfer from epipelagic zooplankton biomass to migrant zooplankton after an increase in productivity in shallower layers.

Factors affecting active flux

We found a significant correlation between net primary production and zooplankton migrant biomass (Supporting Information Fig. S2b), showing the dependence of migrant biomass upon productivity in the upper layers of the ocean. The relationship between primary production and active flux was, however, different during spring and fall, as it was directly related to the respiration rates of organisms in the mesopelagic zone. Respiratory flux during fall was rather low compared with values found during spring, promoting a significant ($p < 0.01$) but low correlation ($r^2 = 0.257$) with primary production (Supporting Information Fig. S2c). Active flux was markedly higher during spring in the mesopelagic zone despite the similar migrant biomass during both seasons (Table 2).

The higher specific ETS values in the mesopelagic zone during spring than during fall (Fig. 5) could be due to (1) differences in temperature between both seasons in the 200–800 m layer, (2) a higher activity of organisms due to enhanced feeding there, (3) the smaller body size of zooplankton organisms during the spring season, or (4) a combination of the previous factors. Temperature is one of the most important drivers of zooplankton respiration rates in the ocean (Ikeda 1985).

However, the temperature in the mesopelagic zone in our study was quite similar during both sampling periods and even slightly lower in the northern transect (Supporting Information Fig. S3). Therefore, we rule out temperature as a driver of the higher specific ETS activity in the mesopelagic zone.

The observed higher ETS activity of organisms at depth due to a higher feeding activity of zooplankton is plausible as an effect of the late winter bloom in subtropical waters. In these waters, Chl *a* and primary production increase during February–March and remain relatively high until April–May (Couret et al. 2023), decreasing thereafter as a result of stratification (De León and Braun 1973; Fernández de Puelles and García-Braun 1989). Also, epipelagic abundance and biomass of phytoplankton and zooplankton were found to increase during the same period (Hernández-León et al. 2004; Schmoker and Hernández-León 2013; Garijo and Hernández-León 2015; Armengol et al. 2020). Even the specific ETS activity of zooplankton remained high during April–May in the euphotic zone (Hernández-León et al. 2004). Thus, the annual injection of nutrients during winter–spring in these waters (De León and Braun 1973; Cianca et al. 2007; Neuer et al. 2007) is suggested to promote the transport of energy and matter to deeper layers, as also suggested by Putzeys et al. (2011) in their study of active flux after the bloom period in subtropical waters.

Body size is another factor that could promote the higher values of specific ETS activity in the mesopelagic zone. It is known that zooplankton respiration rates are also related to body size (Ikeda 1985). Smaller organisms also display higher specific ETS activities, as expected from a respiration rate proxy (Bode 2011). Thus, the differences we found in specific ETS activity in the mesopelagic zone between spring and fall could also be an effect of differences in zooplankton body size among seasons (Fig. 6; GAM results). In fact, higher specific ETS activities were observed in the upper mesopelagic zone (Fig. 5), coinciding with smaller organisms there during spring (Fig. 6), while lower values during fall coincided with a larger body size of the organisms.

The smaller size of zooplankton organisms could also promote a higher active flux value than the estimates shown in this study. In fact, we applied a conservative respiration/ETS (R/ETS) ratio of 0.5 in our study, but higher R/ETS ratios were found in zooplankton of smaller size classes (Hernández-León and Gómez 1996). Thus, a higher R/ETS ratio during spring would promote higher respiration rates and, therefore, zooplankton respiratory flux. This is also supported by the higher R/ETS ratio found in the Canary Island waters at high primary production (Hernández-León and Gómez 1996). Moreover, an R/ETS ratio near 1.0 was obtained for migrant copepods by Hernández-León et al. (2019*c*), supporting the use here of a rather conservative estimate of respiration rate. In this way, the total active flux estimated in this study would promote a higher value of the active/passive flux ratio during the productive period in subtropical waters.

Passive vs. active flux

The results support the finding from Hernández-León et al. (2019*a*) of an important role of the mesopelagic fauna in areas of high productivity in oceanic waters. They found low passive flux in a transect from the quite oligotrophic waters off Brazil to the mesotrophic and eutrophic waters of the Guinea Dome and the oceanic upwelling system off Northwest Africa. However, in coastal upwelling waters, although active flux is also high, gravitational flux is much higher due to the dominance of diatoms there (Stukel et al. 2023). There is also compelling evidence of a greater role of zooplankton in the downward transport of carbon related to the productivity in the upper layers of the ocean, as stated by Hernández-León et al. (2020). They found higher biomass in the mesopelagic and bathypelagic zones related to net primary production in shallower layers at the global scale in tropical and subtropical waters.

Here, we provided evidence of an enhanced transport by zooplankton active flux during spring compared with fall, which is related to seasonality, suggesting an important role of the migrant fauna compared with gravitational flux (Table 2). The role of DVM in the transport of carbon to the mesopelagic and bathypelagic zones is poorly known mainly because of data paucity due to both the gap in zooplankton sampling during the day and night in oceanographic cruises and the difficulties associated with sampling the deep sea. Recent modeling efforts showed that active flux in the ocean increases the downward carbon transport by 10–18% at the global scale (Aumont et al. 2018; Archibald et al. 2019; Nowicki et al. 2022), exporting carbon for an average time of 150 yr. Hernández-León et al. (2019*a*) found zooplankton and micronekton transporting about 25% of passive plus active flux in oligotrophic waters. As most of the ocean surface is oligotrophic, their values matched the model results considering that 20% is transported due to physical mixing (Nowicki et al. 2022). However, they also found striking differences in productive environments. Active flux by zooplankton and micronekton accounted for > 80% of the passive plus active flux in mesotrophic and eutrophic zones of oceanic waters (fig. 10 in Hernández-León et al. 2019*a*). These high values agree with the results of Stukel et al. (2018) in the Costa Rica Dome, an open-ocean upwelling zone, where most of the flux was driven by the pelagic fauna. In our study, we show that during the productive season, active flux is also higher than passive flux (Table 1), supporting the important role of zooplankton in transporting carbon downward in productive areas of the ocean.

In summary, the increase in zooplankton biomass in the mesopelagic and bathypelagic zones in areas of higher primary production as observed by Koppelmann and Weikert (2007) in the Mediterranean Sea and by Hernández-León et al. (2020) at the global scale, suggested that a bloom in the upper layers of the ocean is shunt to the deep sea, fueling animal communities there. Here, we observed an increase in metabolism in the mesopelagic zone after the productive period in the epipelagic layer of subtropical waters. The higher specific ETS activity was related to the zooplankton community structure, as indicated by the lower body weight of organisms in the mesopelagic layer during spring. Thereafter, during fall, body weight and biomass increased in deep waters as fingerprints of a more stable and mature system. Our review of the respiratory flux around the Canary Islands also showed that the flux values were fourfold higher during May than during the stratified season. Thus, models accounting for active flux should consider the higher active transport in areas with higher primary production, as well as the effect of seasonality described above. In any case, further research is needed to unveil the effect of this small and seasonal increase in primary production in subtropical waters (about 70% of the ocean) on the active flux by zooplankton and micronekton. Productivity explains the rather large differences in zooplankton active flux observed in the literature (Hernández-León et al. 2019*a*) but, as observed here, this flux in oceanic waters could be larger than the gravitational flux under a productive scenario.

Data availability statement

Datasets generated and/or analyzed during the current study are available at PANGAEA (Hernández-León et al., 2024), https://doi.pangaea.de/10.1594/PANGAEA.965910.

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Conflict of Interest

None declared.

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