



## Active flux seasonality of the small dominant migratory crustaceans and mesopelagic fishes in the Gulf of California during June and October

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### ABSTRACT

The biological carbon pump is the process that transports carbon vertically out of the mixed layer in the ocean. Besides the sinking flux of organic particles, active flux due to the daily vertical migration of zooplankton and micronekton promotes a significant carbon transport not fully accounted for or understood in the world's oceans. The diversity and abundance of epipelagic and mesopelagic species in the Gulf of California has been extensively studied, but the role of micronekton in carbon export has not yet been investigated. We studied the carbon flux promoted by juvenile and adult mesopelagic fishes and crustaceans (Decapoda and Euphausiidae) during the transition from the cold to warm period (June) and the onset of the warm season (October) in 2018. We provide the first estimation of migrant biomass and respiratory flux of the most abundant migratory species of mesopelagic fishes, decapods and euphausiids in the Gulf of California. The micronekton species collected accounted for a large biomass of mesopelagic fishes and pelagic crustaceans. The average migrant biomass estimates were  $151.5 \pm 101.2 \text{ mg C}\cdot\text{m}^{-2}$  during June and  $90.9 \pm 75.3 \text{ mg C}\cdot\text{m}^{-2}$  during October. The enzymatic activity of the electron transfer system (ETS) was measured as an estimate of their respiratory rates. Average specific ETS activity was significantly different between fishes and decapods, and between fishes and euphausiids ( $p < 0.05$ ). The respiratory flux of fishes was predominant in the Gulf of California, followed by pelagic decapods and euphausiids. Seasonal changes in respiratory flux were observed for fishes (June:  $6.1 \pm 1.5 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ; October:  $3.2 \pm 1.8 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) and decapods (June:  $0.4 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ; October:  $0.7 \pm 0.05 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ). Respiratory flux estimation by crustaceans (decapods and euphausiids) and fishes together was  $6.86 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  during June, and  $4.21 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  during October 2018, suggesting a functional role of this large micronektonic fauna in the biological carbon export in this region.

### 1. Introduction

The biological carbon pump (BCP) drives the transport of organic matter resulting from photosynthesis in the euphotic zone to the deeper meso- and bathypelagic layers (Volk and Hoffert, 1985; Lampitt et al., 2008; Pakhomov et al., 2018). The vertical transfer processes include the passive gravitational sinking of particulate organic carbon (POC),

diffusion and advection of dissolved organic carbon (DOC), and active carbon transport due to the daily vertical migration of pelagic animals (Buesseler et al., 2007). Vertical migrants actively transport organic matter consumed near the surface by zooplankton and micronekton (mainly fishes, decapods, and cephalopods) at night to their daytime residences at depth. This transport is promoted through a combination of respiration, excretion, defecation, sinking of moults in crustaceans,

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eggs of broadcast spawning species, and mortality at depth (Lampert, 1989; Longhurst, 1991; Zhang and Dam, 1997; Steinberg and Landry, 2017). Active transport of biomass performed by zooplankton has been the subject of numerous studies around the world (Longhurst, 1991; Zhang and Dam, 1997; Steinberg et al., 2002; Hernández-León et al., 2001, 2019a, 2019b), but there is still limited knowledge and understanding of the micronekton contribution to the biological carbon pump (e.g., Angel, 1989; Hidaka et al., 2011; Ariza et al., 2015; Sarmiento-Lezcano et al., 2022; Woodstock et al., 2022).

Micronekton sampling is a time-consuming activity on board oceanographic cruises and requires the use of large nets or trawls that are usually limited by the number of depth strata that can be sampled. Active avoidance of nets by fast swimming micronektonic species also limits their effective sampling (Kaartvedt et al., 2012). So, knowledge about the ecological function of these organisms in the biological carbon pump is rather scarce. The active flux of micronektonic species have been studied in different oceanic regions such as the western Equatorial Pacific (Hidaka et al., 2001), the subtropical Northeast Atlantic (Angel and Pugh, 2000; Ariza et al., 2015), the tropical and subtropical Atlantic (Hernández-León et al., 2019a) and the Southern Ocean (Belcher et al., 2019, 2020). However, there is still limited information about micronektonic organisms and their ecological role in active flux in relation to seasonal changes (Belcher et al., 2019). Productivity in the ocean changes seasonally as the phytoplankton blooms extend from subtropical waters, the “late winter bloom” (Menzel and Ryther, 1961), to temperate waters during spring (Chiswell et al., 2015), and polar oceans during summer (Stramska, 2005). The seasonal primary production cycle in the central North Pacific Ocean is characterized by a summer increase in primary production rates coupled with a passive export pulse

transporting carbon into the deep sea (Karl et al., 2012; Church et al., 2013). As a result, the meso- and bathypelagic zooplanktonic community also exhibits seasonal variations in biomass and species composition (Hannides et al., 2013). Putzeys et al. (2011) also observed an increase in zooplankton migrant biomass after the late winter bloom in the Canary Current coinciding with a decrease of epipelagic zooplankton biomass. Also, zooplankton transports up to 20 % more carbon during the mid-latitude spring bloom than at equatorial or boreal latitudes (Hansen and Visser, 2016).

These seasonal differences in the biomass of vertical migrants were also reported for migrant micronekton, particularly in lanternfishes (Dypvik et al., 2012; Peña et al., 2021). Belcher et al. (2019) also observed respiratory flux variability for mesopelagic fishes during spring, summer, and autumn in the Scotian Sea. Respiratory flux variability is closely related to daily vertical migration patterns of myctophid species, ice cover, large phytoplankton blooms (e.g., Korb et al., 2008, 2012), and mesozooplankton abundance (e.g., Ward et al., 2012). Thus, the different seasonal scenarios promoted temporal changes in the micronekton downward carbon flux.

The Gulf of California is a productive tropical-subtropical ecosystem (annual integrated primary production  $>300 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) with pronounced seasonal and interannual variability (Álvarez-Borrego and Lara-Lara, 1991; Hidalgo-González and Álvarez-Borrego, 2004; Álvarez-Borrego, 2010). Its phytoplankton productivity is attributed to three main fertilization mechanisms: wind-induced upwelling events, tidal mixing, and exchange of water masses between the Gulf of California and the Pacific Ocean (Rubio-Rodríguez et al., 2018). The north westerly winds that force upwelling along the east coast of the Gulf of California prevail from November to May and generate coastal upwelling along the

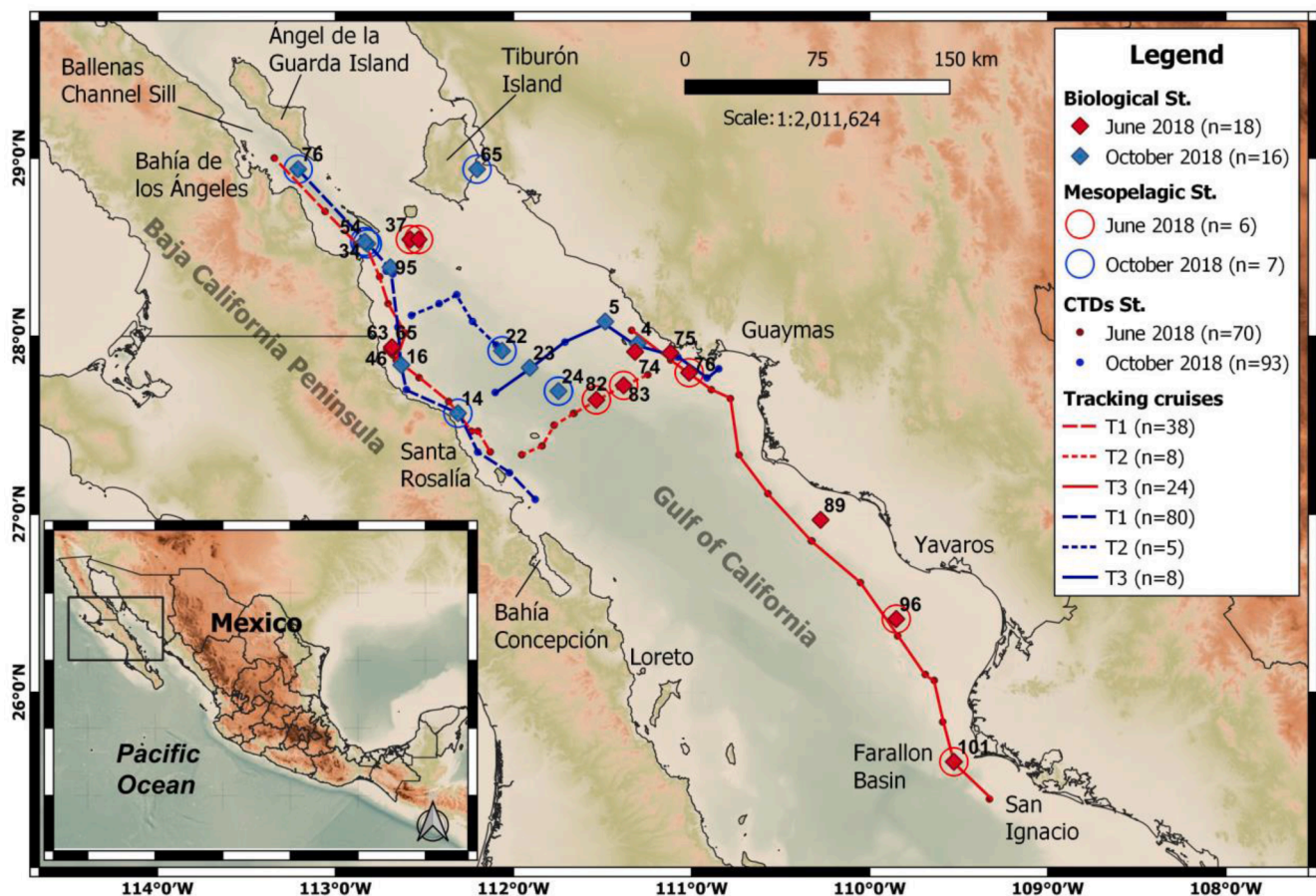


Fig. 1. Location of the area of studied during the oceanographic cruises carried out on board the R/V El Puma during June (red) and October (blue) 2018 at the north-central regions of the Gulf of California, Mexico. Number of sampling stations (n).

east coast of the gulf, and therefore nutrient enrichment, phytoplankton growth, and an increase in net primary production (NPP) (Zeitzschel, 1969). During summer and autumn (June to October), strong thermal stratification precludes upwelling and therefore phytoplankton biomass is generally low (Santa-María-del-Angel et al., 1999). However, intense tide-related mixing is responsible for the high primary productivity in the Midriff Island region (Ángel de la Guarda and Tiburón Islands, Fig. 1) (Álvarez-Borrego and Lara-Lara, 1991). The exchange of water masses at the entrance of the Gulf of California creates oceanographic conditions similar to those of the East Pacific Ocean (Álvarez-Borrego, 1983; Portela et al., 2016). Also, the depth of the mixed layer deepens from summer to winter, which stimulate the vertical diffusion of nutrients to the euphotic zone and establishes a seasonal variability in the vertical structure of the water column (Escalante et al., 2013). Thus, primary production is higher during winter and spring than during summer and autumn, when surface waters are warmer and stratified (Hidalgo-González and Álvarez-Borrego, 2004). The sea surface temperature (SST) is inversely associated with the seasonality of primary production, showing a cold season from December to May, a cold-warm transition period during June, a short warm season from July to October, and a warm-cold transition period during November (Álvarez-Borrego and Lara-Lara, 1991; Hidalgo-González and Álvarez-Borrego, 2004). Although the seasonal variation of primary production in the central and Midriff Archipelago region is well known (Hidalgo-González and Álvarez-Borrego, 2004), there is no information about the active carbon flux of zooplankton and micronekton and its seasonality during periods of high and low primary production.

The Gulf of California holds one of the most diverse and highly endemic ichthyofaunas of the eastern Pacific. The Cortez Province is a zoogeographic region showing a temperate-subarctic fauna in the northern region, and a tropical-subtropical fauna in the southern region of the Gulf of California (Briggs, 1974; Robertson and Cramer, 2009). The oceanographic conditions, geographic location, and geological history deeply influenced speciation processes and explain the high species richness within the Eastern Tropical Pacific (ETP) (Mora and Robertson, 2005; Robertson and Allen, 2008; Palacios-Salgado et al., 2012). Mesopelagic fish abundance, composition, and distribution in the Gulf of California have been well studied in their larval stages (Moser et al., 1974; Aceves-Medina et al., 2003, 2004; Funes-Rodríguez et al., 2006; Sánchez-Velasco et al., 2004, 2009; Urias-Leyva et al., 2018; Camacho-Gastélum et al., 2020). *Benthosema panamense* and *Vinciguerria lucetia* are highly abundant mesopelagic species in the Gulf of California, being an important link in the pelagic trophic web (Santana-Iturríos et al., 2013).

Robison (1968) conducted the first comprehensive distribution study of juvenile and adult midwater fishes (11 families, 22 genera and 26 species) in the Gulf of California using a Tucker opening-closing pelagic trawl. Thirteen euphausiid species inhabit the Gulf of California (Brinton and Townsend, 1980; Ambriz-Arreola et al., 2017). The vertical distribution of euphausiid species in the Gulf of California is well known, with *Nyctiphanes simplex* and *Nematoscelis difficilis* being the most abundant krill species in the gulf (Tremblay et al. 2010; Lavaniegos, 1996; Ambriz-Arreola et al., 2017). The pelagic decapod species of the genera *Phasiphaea* and *Maryprocessa* were also reported in the north and central zone off the Gulf of California with *Phasiphaea pacifica* being the most abundant species in this region (Hendrickx, 2012, 2013; Flores-Anduaga and Hendrickx, 2014). Amphipods, cephalopods, mysids, siphonophores, and thaliaceans are also ecologically relevant but typically less abundant (Brinton et al., 1986; Lavaniegos and López-Cortés, 1997; Brusca et al., 2005).

Migrant zooplankton and micronekton are relevant components of the daily vertically migrant biomass (Catul et al., 2011; Ariza et al., 2015), playing an important function in driving the flux of carbon to the deep ocean. Mesopelagic fishes (McGinnis, 1982; Hulley, 1990; Catul et al., 2011), euphausiids (Lavaniegos, 1996; Färber-Lorda et al., 2010; Tremblay et al., 2010; Ambriz-Arreola et al., 2017), and pelagic

decapods (Childress, 1975; Schalk, 1988; Ikeda, 2014; Herrera et al., 2019) perform diel vertical migrations (DVMs) in the Gulf of California. However, as stated above, little is known about the seasonal variability of migrant biomass and respiratory flux performed by these micronektonic organisms. We propose the hypothesis that the large biomass of dominant mesopelagic fishes and crustaceans during June (transition of cold-warm period) and October (onset of the warm season) significantly contribute to the seasonal variability of carbon flux in the Gulf of California. We compare biomass and active carbon flux of several numerically dominant mesopelagic juvenile and adult fish, decapod, and euphausiid species during June and October 2018 in the north-central region of the Gulf of California. Their metabolism was assessed using the enzymatic activity of the electron transfer system (ETS) as a proxy of their respective respiration rates (Packard, 1971). We aimed to study the seasonality of this vertical biomass transport in order to gain knowledge of the magnitude of micronekton carbon flux in the Gulf of California, to provide a basis for biological pump activity of dominant migratory crustaceans and mesopelagic fishes in this system.

## 2. Methods

### 2.1. Survey and hydrography

Micronektonic specimens were collected during two oceanographic cruises from 18th to 28th June 2018 (CAPEGOLCA XIII), and from 14th to 25th October 2018 (CAPEGOLCA XVI) on board the R/V El Puma (UNAM). A total of 74 biological and hydrographic stations were sampled during both oceanographic surveys collecting hydrographic information in the upper 300 m water column during the nighttime (20:00–05:00 h local time) (Fig. 1). Depth, temperature, and conductivity were recorded with a Star-ODDI CTD attached to the Bongo net during the first survey and half of the second one (stations 36–101), and additionally with a calibrated SeaBird SB11 CTD attached to an oceanographic rosette for stations 4–95 during October 2018. Dissolved oxygen concentration was recorded using a Seabird SB-43 sensor and fluorescence was recorded with a Turner Designs 10-AU-005-CE sensor. The oceanographic conditions were contrasted between June and October 2018. June is the cold-warm transitional period, and October is the onset of the warm period (July–October) according to SST and Chl-*a* concentration seasonal phenology (Álvarez-Borrego and Lara-Lara, 1991; Hidalgo-González and Álvarez-Borrego, 2004). Three transects were performed during each oceanographic cruise: Western coast (T1), Centre of the Gulf of California (T2), and Eastern coast (T3) (Fig. 1). The temperature-salinity diagram (T-S) was used to identify the sea water mass in the study area according to the water masses criteria reported in Portela et al. (2016). The vertical distribution of temperature and chlorophyll-*a* were visualized using Ocean Data View (Schlitzer, 2021).

### 2.2. Bongo net sampling

All specimens were collected during the nighttime (20:00–05:00 h local) using a standard Bongo net (0.61 m mouth diameter, 505 µm mesh net) equipped with a General Oceanics model 2030R digital flowmeter. The integrated layer from maximum depth to surface (32–272 m) was evaluated through oblique hauls for each cruise following standard sampling methods (Smith and Richardson, 1977). The bulk of the migrating scattering layer (MSL) in the Gulf of California is located between 200 and 350 m during the day and above 100 m depth during nighttime (Cade and Benoit-Bird, 2015). Thus, the Bongo net samplings were carried out exclusively at night, towing the net in the 0–300 m layer, where zooplankton and mesopelagic micronekton are distributed during night. The collected specimens were identified on board to the lowest possible taxonomic level and those selected for electron transfer system (ETS) activity analysis (see below) were immediately frozen in liquid nitrogen contained in a 20 L carboy for posterior chemical analyses in the land-based laboratory. After the identification of species,



specimens in good conditions and differences sizes class were selected for ETS analysis. Wet mass (WM) including stomach content and standard length (SL) were measured at the land-based laboratory with an electrical balance (COBOS, AUW 220D  $\pm$  0.01 g). Sex was determined for all fish specimens by macroscopic observations of gonad morphology using a Carl Zeiss Stemi stereomicroscope (Murua et al., 2003; Brown-Peterson et al., 2011). Individuals whose sex could not be determined were called indeterminate. We converted wet mass (WM) to dry mass (DM) using averaged conversion factors obtained for fishes (DM/WM = 5.88) and decapods (DM/WM = 4.82) reported by Childress and Nygaard (1974, 1973), and for euphausiids (DM/WM = 4.37) with the conversion factor provided by Kiørboe (2013). A later conversion from DM to C units was based on the assumption that C content is 40 % of the DM (Bailey et al., 1995; Gómez-Gutiérrez et al., 2012). The proportion of the sampling stations in which the species were present (Frequency of occurrence, %FO) was estimated during both cruises (June n = 18 and October n = 16 zooplankton Bongo net samples). The number of individuals counted in each Bongo haul was expressed as individuals per m<sup>2</sup> according to the water filtered and depth interval (total number of organism  $\times$  depth interval/volume of water filtered). The biomass was estimated using the total mass of each species (total mass of a species  $\times$  depth interval/volume of filtered seawater), and all species for which biomass was calculated were described in the literature as vertical migrants (Schmitt, 1921; Frost and McCrone, 1979; Lavaniegos, 1996; Santana-Iturríos et al., 2013; Ambriz-Arreola et al., 2017). Therefore, we consider the estimated biomass (total mass) of a species per sampling station as its potential migrant biomass. Values for migrant biomass are only given for stations with a seafloor depth > 450 m depth. The capture efficiency of the Bongo net for micronekton is unknown; therefore, we used a conservative net capture efficiency of 50 % and recalculated the potential migrant biomass accordingly.

### 2.3. Electron transfer system (ETS) activity and respiratory flux

Electron transfer system (ETS) activity was estimated in a land-based laboratory. Each individual was homogenized in phosphate buffer (0.05 M PO<sub>4</sub>) keeping the temperature at 0–4 °C to avoid enzyme or protein degradation. ETS activity was determined using the standard method of Packard (1971) subsequently modified by Gómez et al. (1996). The homogenate was centrifuged thereafter at 4000 rpm at 0 °C for 10 min. An aliquot was subsampled and incubated at 18 °C using NADH, NADPH, succinate, and a tetrazolium salt (INT) as the artificial electron acceptor. The incubation was stopped after 20 minutes with a quench solution. The ETS activity was estimated spectrophotometrically at 490 nm wavelength with a turbidity baseline of 750 nm. The ETS activity was corrected for *in situ* temperature (i.e., the estimated temperature of the depth where the migrants reside during the day) using the Arrhenius equation and an activation energy of 15 kcal·mol<sup>-1</sup> (Packard et al., 1975). We used protein content as a proxy for body biomass, which we determined using the method of Lowry et al. (1951) modified for microanalysis by Rutter (1967) and using bovine serum albumin (BSA) as the standard. We converted protein (Prot) into dry mass using the average DM/Prot ratio of 2.21 for fishes and 2.48 for pelagic crustaceans as given by Bailey et al. (1995).

Fish and crustacean respiration rates (R) were estimated from the ETS activities assuming a conservative R/ETS ratio of 0.5 (Ikeda, 1989). This result was converted into carbon units by a stoichiometric calculation (22.4 LO<sub>2</sub> = 12 g C) and a respiratory quotient (RQ) of 0.90 (Brett and Groves, 1979). Daily respiration rates (d<sup>-1</sup>) were obtained from mass-specific respiration rates ( $\mu$ l O<sub>2</sub>·mg prot<sup>-1</sup>·h<sup>-1</sup>) using the above-mentioned respiratory quotient and the conversion factors between protein, dry mass, and carbon. According to the diel vertical migration of organisms in the region (Cade and Benoit-Bird, 2015), hourly estimates were converted to daily rates assuming mesopelagic migrants reside 12 h at depth during the day (200–350 m) and 12 h in the euphotic zone at night (<200 m). Therefore, ETS activities were

corrected with the temperature at these depths. Respiration rates (d<sup>-1</sup>) for species of each taxonomic group were multiplied by the migrant biomass to obtain the respiratory flux for each species in terms of mg C·m<sup>-2</sup>·d<sup>-1</sup>. Net primary production (NPP) was obtained from remote sensing data from the Ocean Productivity web site (<https://www.science.oregonstate.edu/ocean.productivity/index.php>) for the specific dates of the two cruises and the location of the oceanographic stations and processed using the Vertical Generalized Production Model (VGPM).

Statistical analyses (ANOVA) were applied to identify significant differences in the net primary production between June and October, in ETS activity and respiration among species. The Tukey's Honest Significant Differences Post Hoc test (HSD) was used to assess statistical differences between pairs of groups (order, species, sex in fishes, and sampling stations) of the analysis of variance previously applied. The *t*-tests were applied to identify significant differences in carbon content, wet mass, and dry mass between species. All analyses were performed in the programming language R (R Core Team, 2021). The sampling map was generated using the geographic information system QGIS (V.3.22.3) (QGIS Development Team, 2022).

## 3. Results

### 3.1. Hydrographic conditions

The temperature-salinity diagrams (*T-S*) allowed us to identify the Tropical Surface Water (TSW;  $S < 34.6$ ;  $T > 25.1$  °C), Subtropical Sub-surface Water (StSsW;  $34.6 < S < 35.1$ ;  $18 < T < 9$  °C), the Gulf of California Water (GCW;  $S > 35.1$ ;  $T > 12$  °C), and the Transitional Water (WT) with intermediate characteristic of TSW and CCW, according to the criteria described in Portela et al. (2016) (Fig. S1). A sharp stratification was observed in the vertical distribution of temperature in both seasons (Fig. S2). During June, the GCW promoted a deeper thermocline and high salinity values (35.2–35.6) near the Midriff Islands region (stations 42–60 of transect 1 in Fig. 2) associated with eutrophic waters (see below). The StSsW was observed at a depth below 100 m, next to the east coast of the Gulf of California where salinity ranged between 34.5 and 34.9. The thermocline, halocline, and oxycline were shallower in the centre and east coast of Gulf of California (stations 62–100 in transect 2 and transect 3 shown in Fig. 2) than in the west coast during June. Similar hydrographic conditions were observed during October 2018. During this month the GCW and StSsW were observed below 100 m depth in transect 3. Higher Chl-*a* concentrations were found in the upper 50 m of the water column near the Midriff Islands region associated with intense tidal mixing currents typical of this region during both seasons (transect 1, west coast of the Gulf of California in Fig. 2). However, Chl-*a* concentrations increased south of the Midriff Archipelago (transect 2 in Fig. 2) during October. Net primary production was significantly higher during October (796.9–3577.4 mg C·m<sup>-2</sup>·d<sup>-1</sup>; average  $2155.6 \pm 962.6$  mg C·m<sup>-2</sup>·d<sup>-1</sup>) than during June (488.8–1126.5 mg C·m<sup>-2</sup>·d<sup>-1</sup>, average  $743.2 \pm 180.5$  mg C·m<sup>-2</sup>·d<sup>-1</sup>) ( $F_{1,30} = 24.86$ ,  $p < 0.001$ ).

### 3.2. Species abundance, biomass, occurrence, and size structure

Three main mesopelagic fishes (Myctophidae: *Benthoosema panamense* (n = 24) and *Triphoturus mexicanus* (n = 45); Phosichthyidae: *Vinciguerria lucetia* (n = 7)), two main pelagic decapods (Processidae: *Marypprocessa pippinae* (n = 13) and Phasiphaeidae: *Phasiphaea pacifica* (n = 3)) and adults of two euphausiid species (Euphausiidae: *Nematoscelis difficilis* (n = 27) and *Nyctiphanes simplex* (n = 94)) were collected during June and October 2018 (Table S1). There were significant interspecific differences in carbon content between fish species (*V. lucetia* and *B. panamense*,  $p < 0.05$ ); (*V. lucetia* and *T. mexicanus*,  $p < 0.05$ ) (Table S1). However, no significant intraspecific differences in carbon content with sex of mesopelagic fishes were found (One-way ANOVA test,  $p > 0.05$ ). Decapods and euphausiids showed significant differences



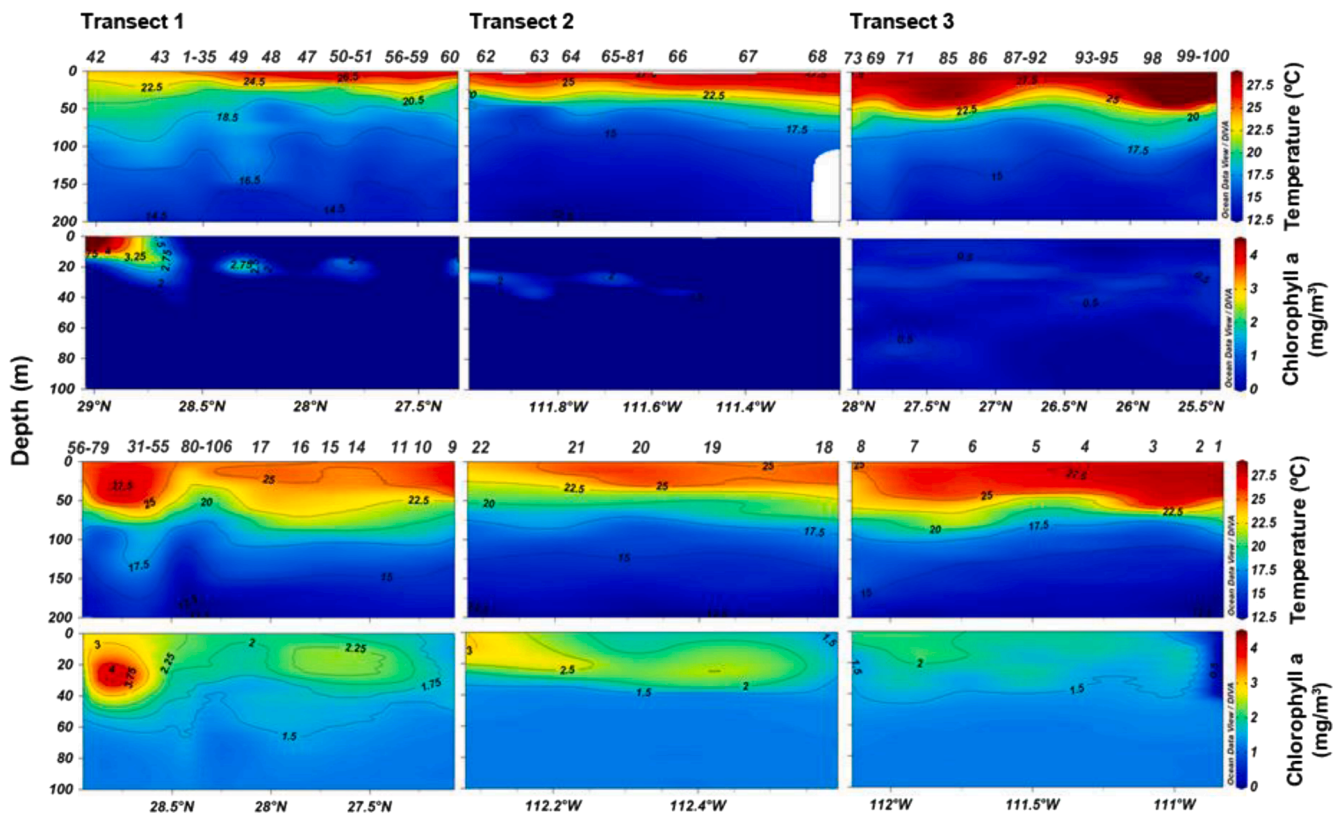


Fig. 2. Vertical distribution of temperature (°C) and chlorophyll-a concentration (mg/m<sup>3</sup>) during June (upper panels) and October (lower panels) 2018 across the Gulf of California. Observe the higher values of chlorophyll-a during October compared to June.

within each taxon in carbon content (Table S1;  $p < 0.05$ ). The highest abundances were found for euphausiids, accounting for 78 % of the total micronekton collected with the Bongo net during June and 38 % during October 2018 (Table 1), while the relative abundance of mesopelagic fish was 12 % in June and 26 % in October. Relative abundance of decapods accounted a 9 % during June and 35 % in October. Mesopelagic fishes were the main contributors to biomass in June (67 %) and October (61 %), followed by euphausiids in June (23 %) and decapods in October (27 %) (Table 1). Fishes and decapods had a higher frequency of occurrence in October than in June, while euphausiids were more frequently collected in June than in October.

The mean migrant biomass (using a net capture efficiency of 50 %) was not significantly different between June and October (June  $151.48 \pm 101.19 \text{ mg C}\cdot\text{m}^{-2}$ ; October  $90.89 \pm 75.34 \text{ mg C}\cdot\text{m}^{-2}$ ) ( $F_{1,18} = 2.365$ ,

$p = 0.14$ ). The largest contribution to the migrant biomass had mesopelagic fishes followed by juvenile and adult decapods and adult euphausiids during both cruises (Tables 2, 3). The migrant biomass of fishes was higher in the central area of the Gulf of California during June than other surveyed areas (Fig. 3A). However, migrant biomass during October was higher in the central area than near the Midriff Archipelago (Fig. 3B). The migrant biomass of decapods and euphausiids were below  $150 \text{ mg C}\cdot\text{m}^{-2}$  during both cruises (Fig. 3 A, B).

### 3.3. Specific ETS activity and respiration

Average ETS activities were higher in mesopelagic fishes than in euphausiids and decapods ( $F_{2,107} = 21.33$ ,  $p < 0.001$ ) (Table S2). Differences were significant between fishes and decapods ( $p < 0.05$ ) and

Table 1

Abundance, biomass, and frequency of occurrence (average and standard deviation) of each micronektonic species collected during night in June 2018 (cold-warm transition period,  $n = 18$ ) and October 2018 (in the onset of warm season,  $n = 16$ ). Average of fish, decapods, and euphausiids abundance and biomass (Bold Mean  $\pm$  SD).

		Abundance (Ind. m <sup>-2</sup> )		Biomass (mg DM·m <sup>-2</sup> )		Frequency of occurrence (%)	
		June 2018	October 2018	June 2018	October 2018	June 2018	October 2018
Fish	<i>B. panamense</i>	–	$0.07 \pm 0.18$	–	$7.45 \pm 19.92$	–	19
	<i>T. mexicanus</i>	$0.45 \pm 0.73$	$0.64 \pm 0.94$	$59.53 \pm 91.01$	$66.11 \pm 89.76$	33	56
	<i>V. lucetia</i>	$0.05 \pm 0.14$	$0.05 \pm 0.20$	$6.45 \pm 20.25$	$4.71 \pm 18.84$	11	6
	<b>Mean <math>\pm</math> SD</b>	<b><math>0.62 \pm 0.94</math></b>	<b><math>0.76 \pm 0.95</math></b>	<b><math>90.17 \pm 130.62</math></b>	<b><math>77.83 \pm 92.57</math></b>	–	–
Decapod	<i>M. pippinae</i>	$0.38 \pm 0.84$	$0.80 \pm 1.86$	$10.04 \pm 21.91$	$16.07 \pm 34.45$	28	31
	<i>P. pacifica</i>	$0.10 \pm 0.32$	$0.20 \pm 0.30$	$2.23 \pm 6.95$	$18.37 \pm 32.03$	11	44
	<b>Mean <math>\pm</math> SD</b>	<b><math>0.48 \pm 0.91</math></b>	<b><math>1.01 \pm 1.86</math></b>	<b><math>12.27 \pm 23.01</math></b>	<b><math>34.44 \pm 47.41</math></b>	–	–
Euph.	<i>Ne. difficilis</i>	$0.88 \pm 1.42$	$0.75 \pm 0.98$	$12.59 \pm 22.16$	$9.41 \pm 12.46$	33	31
	<i>N. simplex</i>	$2.62 \pm 3.51$	$0.35 \pm 0.86$	$12.94 \pm 18.07$	$4.74 \pm 11.73$	56	25
	<b>Mean <math>\pm</math> SD</b>	<b><math>4.07 \pm 3.79</math></b>	<b><math>1.10 \pm 1.49</math></b>	<b><math>29.31 \pm 26.99</math></b>	<b><math>14.15 \pm 19.71</math></b>	–	–

**Table 2**

Average temperature at depth and species migrant biomass using 50 % of capture efficiency (CE 50 %), mass-specific ETS activity, respiration at depth by day, and respiratory flux in each oceanographic station of June 2018 (cold-warm transition period). Average of total taxa (**Total Mean ± SD**).

	Station	Station/ Sampling depth (m)	Average Temperature at depth (°C)	CE 50 % Migrant biomass (mg C·m <sup>-2</sup> )	Sp. ETS activity ( $\mu\text{l O}_2\cdot\text{mg}$ $\text{prot}^{-1}\cdot$ $\text{h}^{-1}$ )	Respiration at depth by day			CE 50 % Respiratory flux (mg C·m <sup>-2</sup> ·d <sup>-1</sup> )	Net primary production (mg C·m <sup>-2</sup> ·d <sup>-1</sup> )
						( $\mu\text{l O}_2\cdot\text{mg}$ $\text{prot}^{-1}\cdot$ $\text{h}^{-1}$ )	( $\mu\text{l O}_2\cdot\text{mg}$ $\text{prot}^{-1}\cdot$ $\text{h}^{-1}$ )	( $\mu\text{l O}_2\cdot\text{mg}$ $\text{DM}^{-1}\cdot$ $\text{h}^{-1}$ )		
<b>Fish</b>										
	E76	480/272	13.04	252.8	4.42 ± 1.90	2.21 ± 0.95	1.10 ± 0.43	0.03	7.58	1126.5
	E82	1463/237	12.66	121.3	5.87 ± 0.13	2.94 ± 0.06	1.32 ± 0.03	0.04	4.85	488.8
	E83	878/234	12.91	174.1	5.61 ± 3.14	2.81 ± 1.57	1.27 ± 0.71	0.04	6.96	854.0
	E96	524/169	13.84	338.4	5.43 ± 0.80	2.71 ± 0.39	1.23 ± 0.18	0.02	6.76	491.4
	E101	427/232	12.94	81.42	8.13 ± 3.60	4.07 ± 1.79	1.84 ± 0.81	0.05	4.07	568.8
	<b>Mean ± SD</b>			193.6 ± 103.3					6.1 ± 1.5	705.9 ± 278.7
<b>Dec.</b>										
	E37	914/183	14.16	60.44	0.88 ± 0.42	0.44 ± 0.21	0.20 ± 0.09	0.006	0.36	795.8
<b>Euph</b>										
	E37	914/183	14.16	43.2	0.62 ± 0.42	0.31 ± 0.21	0.14 ± 0.09	0.004	0.17	795.8
	E82	1463/237	12.66	140.2	0.67 ± 0.23	0.34 ± 0.12	0.15 ± 0.05	0.004	0.56	488.8
	<b>Mean ± SD</b>			91.7 ± 68.6					0.4 ± 0.3	642.3 ± 217.1
<b>Total Mean ± SD</b>				151.5 ± 101.2					3.9 ± 3.1	701.2 ± 231.1

between fishes and euphausiids ( $p < 0.05$ ) (Fig. 4). Average ETS activities during June and October was not significantly different for fishes ( $F_{1,75} = 0.89$ ,  $p = 0.14$ , June: 3.01–10.68; October: 0.60–17.97), decapods ( $F_{1,14} = 0.89$ ,  $p = 0.36$ , June: 0.58–1.18; October: 0.73–4.01), or euphausiids ( $F_{1,17} = 1.54$ ,  $p = 0.23$ , June: 0.33–3.43; October: 0.46–3.77). Thus, each taxonomic group seems to have stable ETS activities independent of the time of sampling. Similarly, no significant differences were observed between female and male mesopelagic fishes ( $F_{1,75} = 0.29$ ,  $p = 0.75$ ).

### 3.4. Respiratory flux

Respiratory flux obtained from migrant biomass and respiration rates at depth per day was higher in June than in October ( $F_{1,18} = 4.438$ ,  $p < 0.05$ , June:  $3.9 \pm 3.1$  mg C·m<sup>-2</sup>·d<sup>-1</sup>; October:  $1.6 \pm 1.8$  mg C·m<sup>-2</sup>·d<sup>-1</sup>; Tables 2, 3). The distribution of respiratory flux activities showed higher values near the east coast and in the centre of the Gulf of California for fishes, and near the Midriff Archipelago and in the centre of the Gulf of California for euphausiids and decapods (Fig. 5A, B). Respiratory flux of fishes peaked in the mid-eastern area of the Gulf of California during June (Fig. 5A, S2-A). However, we observed higher respiratory flux in transects 2 and 3 during October, but lower near the Midriff Archipelago (Fig. 5B, S2-B). Respiratory flux of decapods and euphausiids were  $< 1$  mg C·m<sup>-2</sup>·d<sup>-1</sup> during both oceanographic cruises (Fig. 5A, B). Significant differences of respiratory flux were found between June and October in fishes ( $F_{1,8} = 7.203$ ,  $p = 0.03$ ) and decapods ( $F_{1,4} = 34.94$ ,  $p = 0.03$ ), but not in euphausiids ( $p > 0.05$ ) (Tables 2, 3, Fig. 6). The respiratory flux of *T. mexicanus* ( $4.2 \pm 2.5$  mg C·m<sup>-2</sup>·d<sup>-1</sup>) and *V. lucetia* ( $4.9$  mg C·m<sup>-2</sup>·d<sup>-1</sup>) were higher during June than during October (*T. mexicanus*  $3.6 \pm 2.1$ ; *V. lucetia*: 0.6; *B. panamense*  $1.3$  mg C·m<sup>-2</sup>·d<sup>-1</sup>). However,

pelagic decapods (*M. pippinae* and *P. pacifica*) showed higher respiration in October than in June. The euphausiids *N. simplex* and *Ne. difficilis* showed similar values of respiratory flux during both periods. The respiratory flux activities of mesopelagic fishes accounted for 89 % in June and 76 % in October (Tables S2, S3). Therefore, the respiratory flux of decapods represented 6 % in June and 17 % in October and for euphausiids represented 5 % in June, and 7 % in October and the rest was from migrant mesopelagic fishes.

Finally, the respiratory flux of mesopelagic fishes and crustaceans recorded during June and October, using the conservative capture efficiency of 50 %, was highly correlated with migrant biomass ( $r^2 = 0.88$ ;  $p < 0.05$ ;  $n = 21$ ) (Fig. 7A). We also observed significant relationship between net primary production recorded in the study area and migrant biomass ( $r^2 = 0.43$ ;  $p < 0.05$ ;  $n = 20$ , Fig. 7B), and with respiratory flux ( $r^2 = 0.32$ ;  $p < 0.05$ ;  $n = 21$ , Fig. 7C).

## 4. Discussion

In the present study we demonstrated the seasonal variability (June and October) of migrant biomass and respiratory carbon flux of numerically dominant pelagic crustaceans and mesopelagic fishes in the Gulf of California. However, we did not find significant differences in migrant biomass among months although NPP was higher in October (onset of the warm season). A large proportion of migrant biomass, and thus respiratory carbon flux of captured pelagic organisms, was closely associated with the upwelling zone in the Midriff Islands region (eutrophic stations). We observed respiratory flux and migrant biomass positively correlated to the net primary production (Fig. 7) as has been observed in the tropical and subtropical Atlantic Ocean (Hernández-León et al., 2019a, 2019b; Sarmiento-Lezcano et al., 2022). The

**Table 3**

Average temperature at depth and species migrant biomass estimated using 50 % of capture efficiency (CE 50 %), mass-specific ETS activity, respiration at depth by day, and respiratory flux in each station of October 2018 (onset of warm season). Average of total taxa (**Total Mean  $\pm$  SD**).

	Station	Station/ Sampling depth (m)	Average temperature at depth (°C)	CE 50 % Migrant biomass (mg C·m <sup>-2</sup> )	Sp. ETS activity ( $\mu$ l O <sub>2</sub> ·mg prot <sup>-1</sup> · h <sup>-1</sup> )	Respiration at depth by day			CE 50 % Respiratory flux (mg C·m <sup>-2</sup> ·d <sup>-1</sup> )	Net primary production (mg C·m <sup>-2</sup> ·d <sup>-1</sup> )
						( $\mu$ l O <sub>2</sub> ·mg prot <sup>-1</sup> · h <sup>-1</sup> )	( $\mu$ l O <sub>2</sub> ·mg DM <sup>-1</sup> · h <sup>-1</sup> )	(d <sup>-1</sup> )		
<b>Fish</b>										
	E14	560/214	13.19	155.6	4.33 $\pm$ 2.23	2.16 $\pm$ 1.12	0.98 $\pm$ 0.50	0.03	4.67	2818.6
	E22	1000/214	10.17	264.7	3.42 $\pm$ 1.83	1.71 $\pm$ 0.91	0.77 $\pm$ 0.41	0.02	5.29	1853.4
	E24	1000/214	10.12	146.2	3.82 $\pm$ 1.63	1.91 $\pm$ 0.81	0.86 $\pm$ 0.37	0.02	2.92	1465.9
	E34	600/214	13.08	63.16	1.56 $\pm$ 1.37	0.78 $\pm$ 0.68	0.35 $\pm$ 0.31	0.01	0.63	3104.0
	E54	593/229	12.33	77.08	4.31	2.15	0.97	0.03	2.31	3577.4
	<b>Mean <math>\pm</math> SD</b>			141.4 $\pm$ 80.1					3.2 $\pm$ 1.8	2563.8 $\pm$ 879.5
<b>Deca</b>										
	E24	1000/214	10.12	71.92	1.48 $\pm$ 0.78	0.74 $\pm$ 0.39	0.33 $\pm$ 0.17	0.010	0.72	1465.9
	E54	593/229	12.33	146.4	0.78 $\pm$ 0.54	0.39 $\pm$ 0.27	0.17 $\pm$ 0.12	0.005	0.73	3577.4
	E76	970/214	12.63	71.4	1.41 $\pm$ 0.27	0.71 $\pm$ 0.14	0.32 $\pm$ 0.06	0.009	0.64	2358.3
	<b>Mean <math>\pm</math> SD</b>			96.6 $\pm$ 43.1					0.7 $\pm$ 0.05	2467.2 $\pm$ 1059.9
<b>Euph</b>										
	E22	1000/214	10.17	20.86	1.23 $\pm$ 0.67	0.62 $\pm$ 0.34	0.28 $\pm$ 0.15	0.008	0.17	1853.4
	E24	1000/214	10.12	7.8	2.21 $\pm$ 1.77	1.10 $\pm$ 0.88	0.49 $\pm$ 0.40	0.014	0.11	1465.9
	E34	600/214	13.08	61.6	2.03	1.02	0.46	0.013	0.80	3104.0
	E65	970/214	12.48	4.04	0.46	0.23	0.10	0.003	0.01	-
	<b>Mean <math>\pm</math> SD</b>			23.6 $\pm$ 26.4					0.3 $\pm$ 0.4	2844.9 $\pm$ 890.7
	<b>Total Mean <math>\pm</math> SD</b>			90.9 $\pm$ 75.34					1.6 $\pm$ 1.8	2422.2 $\pm$ 845.6

estimation of micronekton carbon flux in the Gulf of California evaluated in the present study during June and October 2018 was higher than in other ocean regions such as the Atlantic Ocean, Scotia Sea and Western Equatorial Pacific (Table S3). This suggests that micronekton has an ecologically relevant role in the biological carbon export in the Gulf of California.

#### 4.1. Abundance, biomass, and size structure

There is a lack of information on the abundance and biomass of mesopelagic species of micronektonic fish, decapods, and euphausiids in the Gulf of California in contrast to the zooplankton component (e.g. Moser et al., 1974; Brinton et al., 1986; Gómez-Gutiérrez et al., 2010, 2012; Ambriz-Arreola et al., 2017). The abundance of mesopelagic fishes was higher than that of decapods and their biomass exceeded that of decapods and euphausiids during June and October 2018, in similar proportions to values reported in different oceanic regions of the world (Hidaka et al., 2001; Ariza et al., 2015; Hernández-León et al., 2019a). Larvae, juvenile, and adult stages of *T. mexicanus*, *B. panamense*, and *V. lucetia* were reported as abundant mesopelagic fishes in the uppermost layers of the Gulf of California during warm periods (Robison, 1968; Moser et al., 1974; Aceves-Medina et al., 2003, 2004; Sánchez-Velasco et al., 2004, 2009; Santana-Iturríos et al., 2013; Gutiérrez-Bravo et al., 2022). The abundance and biomass of decapods were less studied in the Gulf of California and the species found in the present study are numerically dominant in this semi-enclosed sea, at least in the central and southern regions of the sampling area (Hendrickx, 2012, 2013;

Flores-Anduaga and Hendrickx, 2014). The euphausiids *N. simplex* and *Ne. difficilis* were reported as the most abundant species of the 13 species distributed from the surface to 500 m depth in the Gulf of California (Brinton et al., 1986; Brinton and Townsend, 1980; Gómez-Gutiérrez et al., 2010, 2012; Lavaniegos, 1996; Lavaniegos-Espejo and Lara-Lara, 1990; Tremblay et al., 2010; Ambriz-Arreola et al., 2017; Tremblay et al., 2011). Furthermore, *N. simplex* represents the bulk of the biomass of krill species, accounting for on average 75 % of total abundance in the Gulf of California (Brinton and Townsend, 1980; Lavaniegos et al., 1989; Gómez-Gutiérrez et al., 2012, García-Fernández et al., in press). Seasonal variability in the abundance of euphausiids in the epipelagic zones in the present study could be biased by their seasonal migration as *Ne. difficilis* tends to reside in deeper water than *N. simplex* during the cold-warm transition period (June) (Brinton, 1979; Lavaniegos, 1996; Tremblay et al., 2010; Ambriz-Arreola et al., 2017).

The abundance and biomass of micronekton estimated in the present study were lower than studies mentioned above for the central part of the Gulf of California (Robison, 1968; Tremblay et al., 2011; Gómez-Gutiérrez et al., 2012; Santana-Iturríos et al., 2013; Flores-Anduaga and Hendrickx, 2014) mainly due to the different sampling methods and efficiency of the nets used. Our sampling methodology is more efficient for juveniles and adults than larval stages. For instance, a higher catchability with larger nets could be the reason for the higher abundance estimations in Robison (1968) and Santana-Iturríos et al. (2013). The variability in physical (currents, winds, tides, and upwelling), chemical (temperature and oxygen), and biological (spatial and vertical distribution, ontogenetic development, etc.) factors could also account



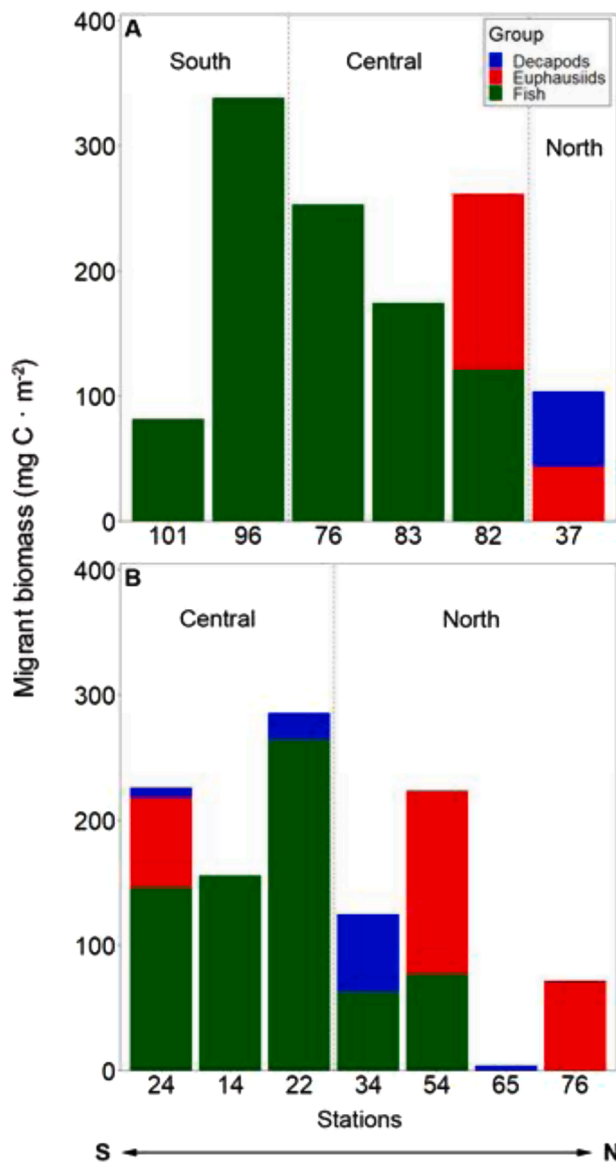


Fig. 3. Micronekton migrant biomass during (A) June and (B) October 2018 assuming a 50% capture efficiency of the Bongo net.

for the observed variations in mesopelagic fish abundance and biomass (Robison, 1968; Santana-Iturríos et al., 2013). The upwelling events along the east coast of the Gulf of California caused by southern winds during June have a weak effect on phytoplankton communities and biomass (low chlorophyll-*a* concentration observed,  $\approx 0.5 \text{ mg} \cdot \text{m}^{-3}$ ), as has been previously observed in the region (Rodén, 1958; Álvarez-Borrego, 2010). This situation may be responsible for the presence and abundances of the mesopelagic fishes around the Midriff Archipelago where tidal mixing maintains an almost continuously high net primary production throughout the year (Mercado-Santana et al., 2017). Also, the abundance and distribution of mesopelagic fishes might be determined by other biological factors such as those related to reproduction, given that these species show marked seasonal abundance and their larvae are found concentrated along the western side of the gulf, decreasing in density towards the east during the cold season (Moser et al., 1974). Horizontal movements within the Gulf of California would explain the differences in biomass among the areas observed (northern, central, and southern).

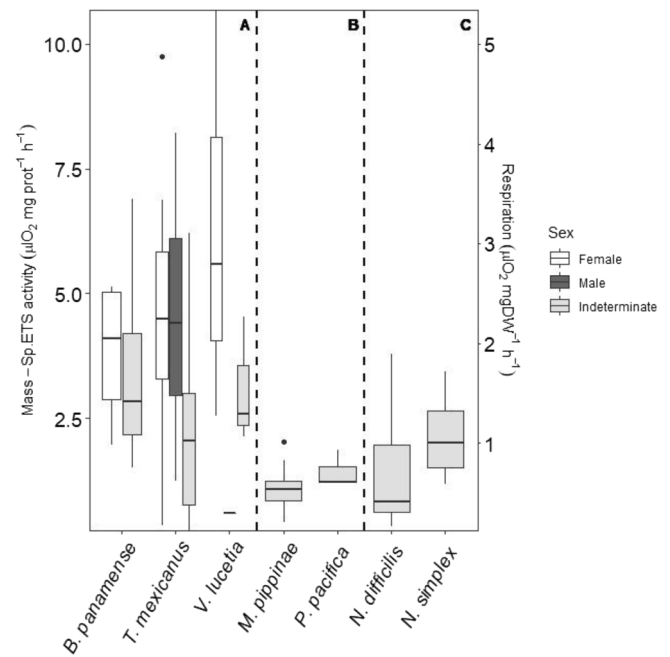


Fig. 4. Mass-specific ETS activity (left y-axis) and respiration (right y-axis) for (A) Mesopelagic fishes; (B) Decapods, and (C) Euphausiids (specimens of June and October 2018 were combined).

#### 4.2. Specific ETS activity

The specific ETS values obtained for micronekton in the present study were slightly lower [mesopelagic fishes ( $3.83 \pm 2.14 \mu\text{L O}_2 \cdot \text{mg prot}^{-1} \cdot \text{h}^{-1}$ ), decapods ( $1.14 \pm 0.45 \mu\text{L O}_2 \cdot \text{mg prot}^{-1} \cdot \text{h}^{-1}$ ) and euphausiids ( $1.54 \pm 1.15 \mu\text{L O}_2 \cdot \text{mg prot}^{-1} \cdot \text{h}^{-1}$ )] than those obtained in the Eastern Tropical Pacific in *Euphausia distinguenda* (Herrera et al., 2019), and for other organisms in different regions of the world oceans (Ariza et al., 2015; Hernández-León et al., 2019a; Belcher et al., 2020). These slight variations may be due to differences in temperature, dissolved oxygen concentration, size, and depth in the Gulf of California. ETS activity is highly dependent on temperature and body size as it is observed in most physiological parameters (Ikeda, 1974, 1989; Vidal, 1980; Hernández-León et al., 2019b; Hernández-León and Ikeda, 2005; Hidaka et al., 2001). Herrera et al. (2019) observed an average value of mass-specific ETS activity of  $1.28 \pm 0.006 \mu\text{L O}_2 \cdot \text{mg prot}^{-1} \cdot \text{h}^{-1}$  in the smaller euphausiid *E. distinguenda* (size range of 6–15 mm) in the 150–400 m depth range, while we found slightly lower mass-specific ETS activity in the range of 0.31–1.10  $\mu\text{L O}_2 \cdot \text{mg prot}^{-1} \cdot \text{h}^{-1}$  (Tables 2 and 3) at similar temperature during the residence depth at day. The body size of specimens and temperature did not change significantly during June and October 2018, but the species collected during both seasons were larger and heavier than those reported by Herrera et al. (2019). Thus, the lower specific ETS activity found in the present study could be related to size, the feeding conditions of these organisms in the Gulf of California, or the influence of the oxygen minimum zone as discussed by Herrera et al. (2019). Taking into account that the energy cost of micronekton swimming decreases with body size, among and within species (Helfman et al., 2009), our ETS values may be influenced by interspecific size.

#### 4.3. Seasonal variability of migrant biomass and respiratory flux

Seasonal changes in the overall micronekton migrant biomass evaluated in the present study (fish, decapods, and euphausiids) between June and October were not statistically significant. However, when analysing each taxonomic group separately, some differences emerged. For example, higher values were observed in June than in October for

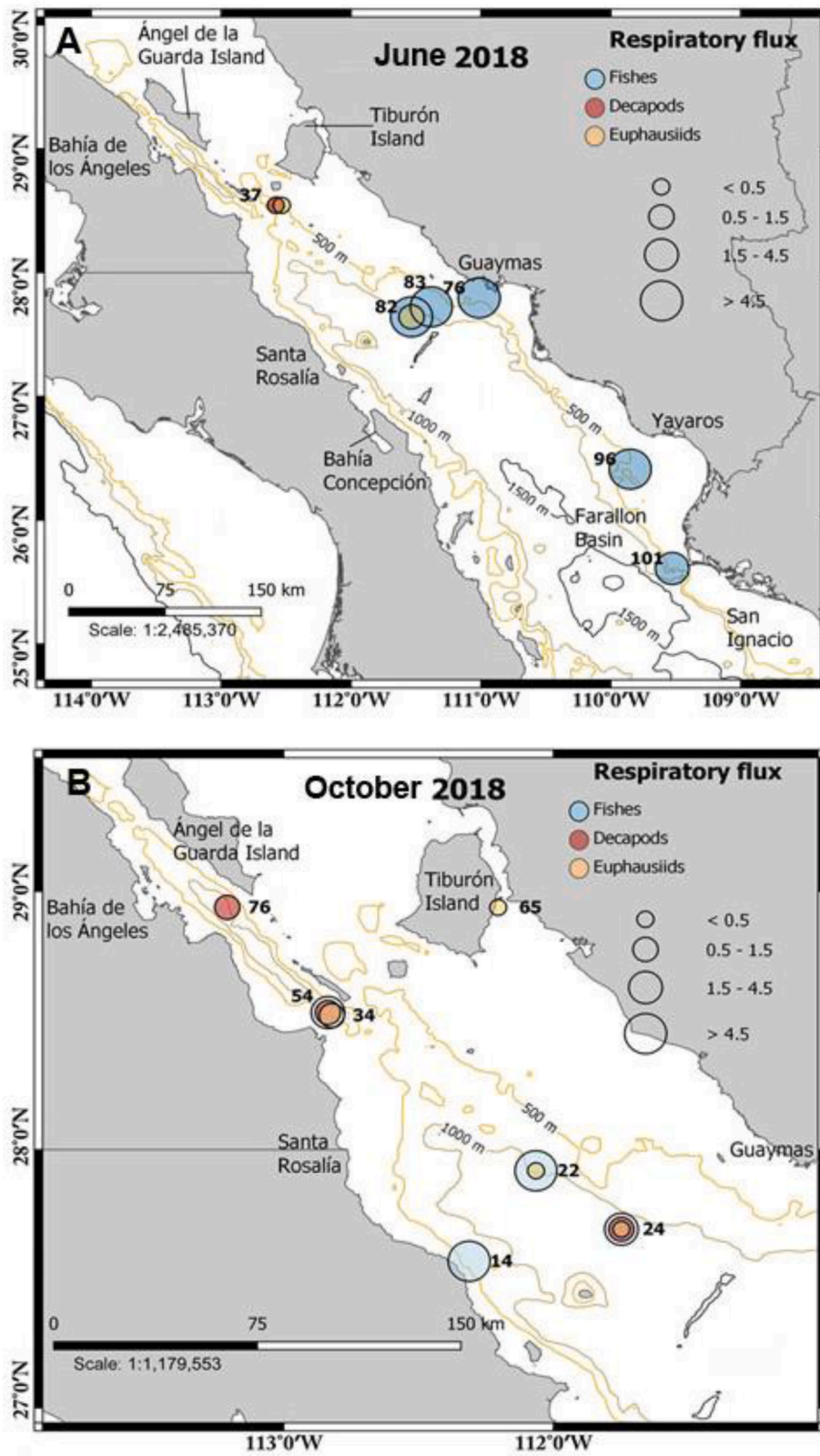


Fig. 5. Distribution of respiratory flux ( $\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) estimated for fishes, decapods, and euphausiids in (A) June and (B) October 2018 in the north-central region of the Gulf of California.

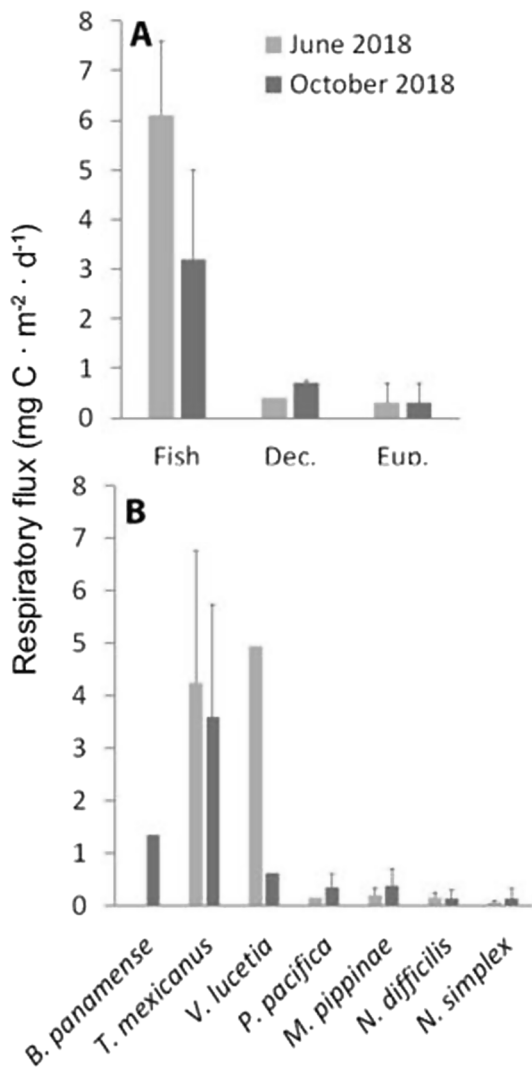


Fig. 6. Respiratory flux estimated during June and October 2018 by (A) fishes, decapods, and euphausiids, and (B) by different species during June and October 2018 (both estimated assuming using a 50% of capture efficiency of the Bongo net).

fishes and euphausiids, but the opposite pattern was observed for decapods. Seasonal variability in seawater temperature, salinity, and wind stress during the spring season could be the reason for the high values of migrant biomass in June, just after the maximum NPP and Chl-*a* concentration occurred during spring (March-May) each year (Hidalgo-González and Álvarez-Borrego, 2004; García-Fernández et al., in press). Data on the seasonality of primary production in the study area (north and central Gulf of California) confirm that it was higher from December-May than July-October (Álvarez-Borrego and Lara-Lara, 1991; Santa-María-del-Angel et al., 1994; Valdez-Holguín et al., 1995; Lluch-Cota, 2000; Cervantes-Duarte et al., 2005). Mesopelagic fish biomass was higher in June during the cold-warm transition period after the Chl-*a* and NPP maximum during spring. The migrant biomass of decapods was, however, higher in October. In general, the average migrant biomass of decapods and euphausiids estimated in Gulf of California were higher than in other regions of the world (Table S3) (Angel and Pugh, 2000; Hidaka et al., 2001; Ariza et al., 2015; Hernández-León et al., 2019a, 2019b; Schukat et al., 2013).

Seasonal variability in respiratory flux has been described for other pelagic fish species and it is related to surface temperature and productivity (Vidal, 1980; Ikeda, 1974, 1989; Hidaka et al., 2001; Hernández-León et al., 2019b), as was observed for mesopelagic fishes

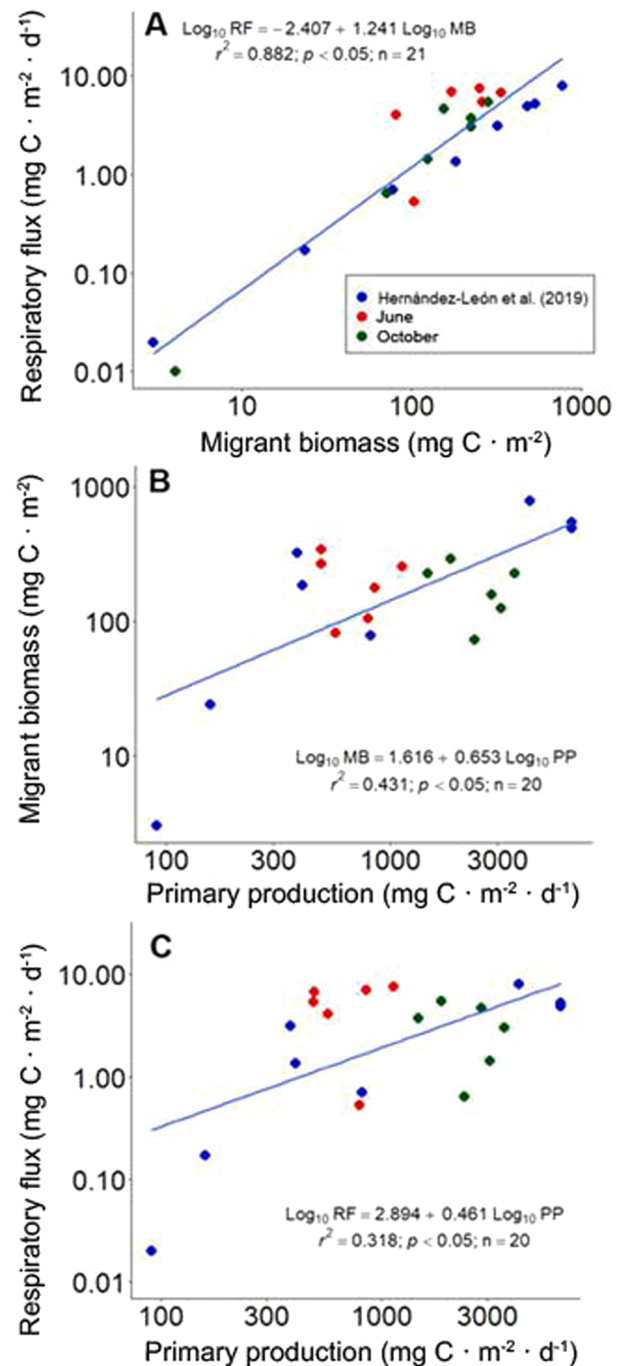


Fig. 7. Relationship of (A) micronekton migrant biomass (using a capture efficiency of 50% of the Bongo net) and respiratory flux, (B) migrant biomass and net primary production obtained from remote sensing, and (C) respiratory flux and net primary production. Blue dots result by Hernández-León et al. (2019a) in the tropical and subtropical Atlantic Ocean. MB, Migrant biomass; RF, Respiratory flux.

and decapods in the north and central of the Gulf of California in the present study. Belcher et al. (2019) showed a latitudinal cline with higher respiration in mesopelagic fishes during spring in the North Scotia Sea, during summer in the Mid Scotia Sea, and during autumn in the South Scotia Sea associated with the large phytoplankton bloom, high mesozooplankton abundances, and ice cover of these regions. We observed eutrophic waters, a shallow thermocline, and an oxycline in the north and centre of the Gulf of California probably causing the increase in migrant biomass and respiratory flux in this region during



June. Therefore, the NPP increase and thermocline deepening (due to a predominance of colder water, StSsW-GCW) during October overall did not affect fish respiration and flux.

The migrant biomass and respiratory flux of euphausiids tended to be similar to that of the mesopelagic fishes, also with maximum values in June (cold-warm transition period). *N. simplex* and *Ne. difficilis* have been previously associated with abundance peaks of phytoplankton and copepods in shallow waters (<50 m depth) (Gómez-Gutiérrez et al., 2012; Palomares-García et al., 2013; Ambriz-Arreola et al., 2017). This may explain the high biomass and respiration values found in the present study in the upper 300 m. Furthermore, the slight differences found between June and October could be related to seasonal vertical migration. *Ne. difficilis* are typically distributed above or below the thermocline, and tend to reside in deeper waters than *N. simplex* during June, while the vertical migration is similar for the two species during the cold season (Lavaniegos, 1996; Tremblay et al., 2010, 2011; Ambriz-Arreola et al., 2017). Decapods showed the maximum respiration flux in October being collected in the most productive zone (Midriff Archipelago) and higher temperatures than those observed in June (Fig. 3 and S2), but these species were also observed within the oxygen minimum zone (OMZ) (Schukat et al., 2013). Several migrant decapod species are known to inhabit areas with low dissolved oxygen concentrations (Childress, 1975), and they are able to regulate their respiration to live anaerobically in the OMZ (Hernández-León et al., 2019b); which would partly explain the similar migrant biomass and respiration flux estimates during both June and October 2018.

Finally, we report the first estimation of crustacean and mesopelagic fish migrant biomass and carbon respiration in the Gulf of California showing higher values during June for mesopelagic fishes and euphausiids, and during October for decapods. Although the present study included a fairly small fraction of marine life present in the Gulf of California, biomass and migrant fluxes values were similar or higher than in other regions (Table S3). We employed a conservative R/ETS = 0.5 in order to compare results with previous studies (Hidaka et al., 2001; Ariza et al., 2015; Belcher et al., 2019, 2020; Hernández-León et al., 2019b; Kwong et al., 2020). However, this R/ETS value is uncertain and needs to be directly estimated in future studies. Hernández-León (2021) suggested a R/ETS = 1 ratio for vertical migrants (micronekton) to solve the differences between assessments based on respiration rates and ETS activities. A seasonal variability in micronekton respiratory flux was found between June and October 2018. However, migrant biomass was not statistically different among seasons, which was probably due to vertical migrations in the sampling area, and shows the importance of studying carbon flux from the epipelagic zone to the deepest zone (mesopelagic and bathypelagic layer) in this tropical-subtropical semi-enclosed gulf.

In summary, we demonstrated that the large biomass of dominant mesopelagic fishes and crustaceans during June (transition of cold-warm period) and October (onset of the warm season) collected with a Bongo net significantly contribute to the seasonal variability of carbon flux in the Gulf of California. Although a larger abundance was observed for adults of pelagic crustaceans (decapods and euphausiids), the mesopelagic fishes represented the largest biomass of micronekton during June and October. Mesopelagic fishes contributed > 50 % to the migrant biomass of the three taxonomic groups during June and October. The average respiratory flux in this semi-enclosed gulf was dominated by mesopelagic fishes, followed by decapods, and euphausiids with a wider range of variability than previously reported in other studies worldwide. Mesopelagic fishes and euphausiids showed an increased respiratory flux in June, in spite of the larger NPP and Chl-*a* concentration during the onset of the warm season (October). The undetermined capture efficiency of the Bongo net, as well as regional oceanographic variability may influence the estimation of zooplankton and micronekton biomass, but this study provides a first estimation of the role of active respiratory flux as a main component of the biological pump in the Gulf of California. Vertical fluxes of zooplankton and

micronekton biomass have been estimated directly through abundance of vertical stratified net samples (Robison, 1972; Ambriz-Arreola et al., 2017) and hydroacoustics (Cade and Benoit-Bird, 2015) but the estimation of active flux seasonality of small dominant migratory crustaceans and mesopelagic fishes provides a baseline for biological pump activity of pelagic organisms, which was previously unknown in the Gulf of California. Understanding the different components of the biological carbon pump in different regions such as the Gulf of California is of paramount importance to assess the role of the oceans in buffering climate change.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The data that has been used is confidential.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2022.102894>.

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