Relative importance of predatory versus non-predatory mortality for dominant copepod species in the northern Chilean (23°S) Humboldt Current System

Sonia Yáñez[1,2], Pamela Hidalgo[1,2,*], Kam W. Tang[3]

[1]Department of Oceanography, Faculty of Natural Science and Oceanography, University of Concepcion, PO Box 160 C, 4030000 Concepción, Chile

[2]Millennium Institute of Oceanography, Faculty of Natural Science and Oceanography, University of Concepcion, PO Box 160 C, 4030000 Concepción, Chile

[3]Department of Biosciences, Swansea University, Swansea SA2 8PP, UK

ABSTRACT: Copepods dominate the zooplankton communities and support large fisheries within the Humboldt Current System (HCS). Using detailed data of live/dead compositions, along with stage durations and molting rates, we derived, for the first time, both predatory and non-predatory mortality rates of the 3 dominant copepod species—*Paracalanus* cf. *indicus*, *Acartia tonsa* and *Calanus chilensis*—within the HCS and examined their relationships with environmental factors. Predatory mortality rates of all 3 species increased linearly with developmental stage, and hence body size, indicating top-down control by predators that prefer larger prey. Intrusion of oxygen-poor water via upwelling and low chlorophyll *a* concentration were linked to increased non-predatory mortality rates of *P.* cf. *indicus* and *A. tonsa*, whereas non-predatory mortality rates of *C. chilensis* were positively correlated with temperature. On average, non-predatory mortality accounted for 34.8–46.3% of the total mortality among the 3 species. Changes in upwelling intensity caused by climate change may alter the extent and patterns of predatory and non-predatory mortalities in the HCS copepod communities.

KEY WORDS: Copepod mortality · Neutral red stain · Copepod carcasses · Vertical life table

1. INTRODUCTION

Mortality is a critical but poorly quantified parameter in copepod population dynamics (Ohman & Wood 1995, Runge et al. 2004). The main cause of copepod mortality is generally assumed to be predation (Verity & Smetacek 1996), but many non-predatory factors can also cause mortality, such as diseases (Delgado & Alcaraz 1999), parasites (Burns 1985, Kimmerer & McKinnon 1990, Ohtsuka et al. 2004), physical and chemical stresses (Roman et al. 1993, Bickel et al. 2011), starvation (Tsuda 1994) and senescence (Ceballos & Kiørboe 2011, Saiz et al. 2015), all of which may leave carcasses behind. Indeed, a meta-analysis of literature data suggests that up to one-third of the mortality in marine pelagic copepods can be attributed to non-predatory causes (Hirst & Kiørboe 2002), and copepod carcasses have been observed around the world, at times in high abundances (Yáñez et al. 2012, 2018, Tang et al. 2014, 2019b).

Recent studies have shown that ignoring even a small magnitude of carcass abundance and non-predation mortality could lead to large errors in population growth and secondary production estimates (Elliott & Tang 2011, Yáñez et al. 2018). Furthermore, predatory mortality represents an upward trophic transfer of copepod biomass, whereas non-predatory mortality represents a potential diversion of copepod production to the microbial loop (Tang et al. 2006, 2009, Bickel & Tang 2010) or sinking fluxes (Sampei et al. 2009, 2012, Ivory et al. 2014, Tang et al. 2019a). Therefore, proper quantification and separation of predatory and non-predatory components of mortality is critical for a more accurate understanding of the pelagic food web. In this regard, the neutral red staining method allows researchers to distinguish between live and dead zooplankton in field samples (Elliott & Tang 2009), thereby providing a means to quantify predatory and non-predatory mortalities (Elliott & Tang 2011, Yáñez et al. 2012, 2018).

The Humboldt Current System (HCS) is among the most productive pelagic ecosystems (Thiel et al. 2007). Copepods dominate its zooplankton communities and support large fisheries in the region (Espinoza & Bertrand 2008). Copepod population abundances within the HCS can be highly variable (Hidalgo et al. 2010, 2012, Pino-Pinuer 2014), but investigation of copepod mortality rates and patterns has been lacking. In northern Chile, Mejillones Bay (23° S) is one of the most important upwelling centers within the HCS (Marín et al. 1993). Shallow cold-water masses with low oxygen concentration (equatorial subsurface water, ESSW) associated with the oxygen minimum zone (OMZ) are present due to upwelling events that occur year-round (Marín & Olivares 1999). The ESSW supports a high zooplankton diversity, with at least 107 species of copepods (Hidalgo et al. 2010), 9 of which are numerically dominant (Escribano et al. 2012). The abundance and biomass of the copepod community in Mejillones Bay are influenced by the vertical distribution of dissolved oxygen (Yáñez et al. 2012), upwelling intensity (Escribano et al. 2009, 2012), upwelling shadow and advection (Giraldo et al. 2002). A recent study suggests that the copepods are highly sensitive to environmental variability, as reflected by changing abundance of copepod carcasses in coastal waters in response to changes in upwelling intensity that reduce or expand the oxygenated surface layer in the HCS (Yáñez et al. 2012).

In this study, we used the neutral red staining method to measure the stage-specific live/dead compositions of the 3 dominant copepod species in the

HCS: *Calanus chilensis*, *Acartia tonsa* and *Paracalanus* cf. *indicus* in the Mejillones Bay (Hidalgo & Escribano 2001, Hidalgo et al. 2010) over 2 annual cycles. From these data, we then, for the first time, calculated and compared their predatory and non-predatory mortality rates and examined their relationships with environmental conditions.

2. MATERIALS AND METHODS

2.1. Field sampling

The study was conducted in northern Chile (Mejillones Bay) within the HCS. Monthly sampling was performed from January 2010 to December 2011 at 3 stations along a coastal transect: Stn 1 (23° 04.2′ S, 70° 25.8′ W; maximum station depth [z_{max}] = 60 m), Stn 2 (23° 02.4′ S, 70° 27.0′ W; z_{max} = 90 m) and Stn 3 (23° 0.2′ S, 70° 28.2′ W; z_{max} = 120 m; Fig. 1). Water temperature, salinity and dissolved oxygen (DO) were measured at each station using an autonomous oceanographic profiler CTD-O SeaBird SBE-19 Plus deployed to 50 m depth. Phytoplankton biomass was measured as concentrations of chlorophyll *a* (chl *a*). Water samples for chl *a* measurements (at 10 and 50 m depths) were obtained using a 5 l Niskin bottle. Chl *a* was measured fluorometrically after filtration onto GF/F (0.7 mm) filters (Morales & Anabalón 2012, Anabalón et al. 2014). Intensity of upwelling was calculated as Ekman transport using the equation of Mann & Lazier (1991):

$$M_x = \frac{\tau_y}{f} \qquad (1)$$

where M_x is Ekman transport (m³ s⁻¹ km⁻¹), f is the Coriolis parameter, and τ_y is along-shore wind stress. M_x is positive for south wind (upwelling) and negative for north winds (downwelling). τ_y was estimated as:

$$\tau_y = \rho_a \times Cd \times (V_y|V_y|) \qquad (2)$$

where ρ_a is air density (1.21 kg m⁻³), Cd is the empirical constant of drag coefficient (0.0014), and V_y is the along-shore wind velocity (m s⁻¹). Ekman transport was averaged monthly from daily estimates based on wind data from the meteorological station at Cerro Moreno airport (https://climatologia/meteochile.gob.cl/)

Copepods were collected by vertical hauls through 0–30 m during the day using a WP-2 net (200 µm mesh and a 50 cm mouth diameter) equipped with a flowmeter. The abundance data were corrected for potential undersampling according to Yáñez et al.
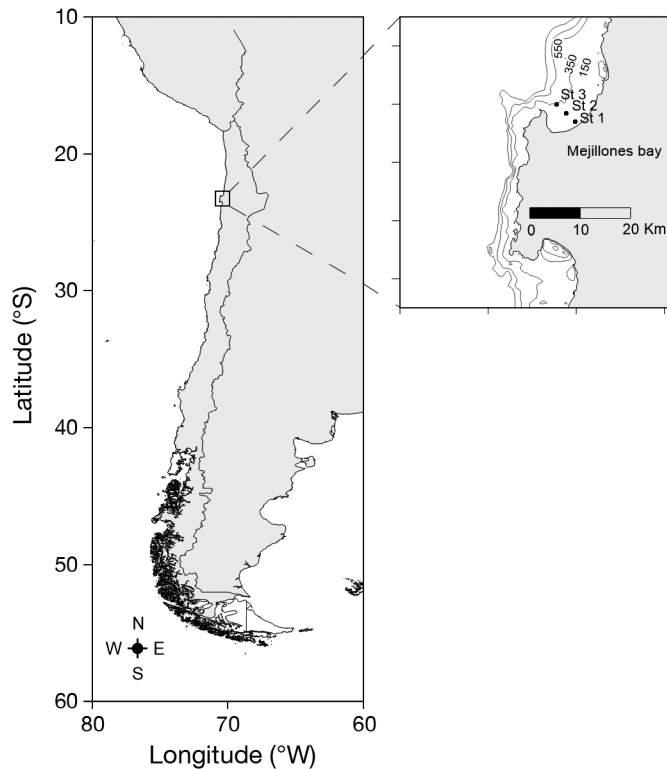
Fig. 1. Upwelling zone in Mejillones Bay (23°S), Chile, where copepod samples were collected

(2018). We applied the correction factors only for C1–C3 stages of *Acartia tonsa* and *Paracalanus* cf. *indicus* and C1 and C2 of *Calanus chilensis* because there were no differences between mesh sizes for the later stages. Our target copepod species are concentrated in this oxygenated upper layer (Hidalgo et al. 2010, Yáñez et al. 2012, Donoso & Escribano 2014, Ruz et al. 2015). Upon retrieval of the net, the samples were transferred to a chilled container and immediately treated with the vital stain neutral red (Elliott & Tang 2009, modified by Yáñez 2009 and Yáñez et al. 2012 for local conditions). Briefly, each sample was incubated with 2–4 ml of neutral red stock solution (0.5% w/v) for 10 min. Afterward, the stained samples were concentrated and briefly rinsed with filtered seawater to remove excess stain, then preserved in 4% neutralized formalin solution in the dark and processed further in the laboratory within 3–6 mo. In the laboratory, the stained samples were concentrated and briefly rinsed with filtered seawater, then acidified by 0.3 ml of 1M acetic acid to develop the stain's color. Under a stereo-microscope (20–40×), the dominant copepod species *P.* cf. *indicus*, *A. tonsa* and *C. chilensis* were counted and identified to developmental stages from entire samples. The

body size was measured using a calibrated reticule (micro-ruler) attached to the eyepiece of the microscope. Individuals that were alive at the time of sampling appeared red, whereas dead ones remained unstained.

2.2. Copepod stage durations

Development times of the different stages were calculated from empirically measured molting rates (Eqs. 2 and 3 in Table S1 in the Supplement at www.int-res.com/articles/suppl/m630p013_supp.pdf). Details of the molting rate experiments were reported by Yáñez et al. (2018). The data were then applied to the equation of Bělehrádek (1935) (Eq. 1 in Table S1) for the relevant environmental temperatures (Table S2) to derive *in situ* stage-specific development times; these development times were used to calculate stage durations (D_i for stage *i*, in days), which were then used to calculate mortality rates.

All 3 copepod species showed significant temporal and ontogenetic differences in stage durations (Fig. S1, Table S3). Stage durations decreased with increasing temperature in all 3 species. For *P.* cf. *indicus* and *C. chilensis*, development progressed with similar stage durations through the early copepodite stages (C1–C3), then slowed through the C4 and C5 stages (i.e. longer stage durations). For *A. tonsa*, development progression was almost identical between C1 and C2, and between C3 and C4, then slowed considerably in C5. Overall, *A. tonsa* tended to have shorter stage durations than the other 2 species for all stages and across all temperatures.

2.3. Predatory and non-predatory mortality rates

We estimated the predatory and non-predatory components of mortality using the vertical life table (VLT) method as modified by Elliott & Tang (2011) by distinguishing between live copepods and carcasses (Table S1). In this method, both live copepods and intact carcasses were treated as survivors of predation, but only live individuals proceeded to the next life stages. Thus, by using both the abundances of live copepods and carcasses, stage duration and carcass turnover rates (Eq. 4 in Table S1), predatory mortality rate and total mortality rates were iteratively solved for (Eqs. 5–7 in Table S1). Non-predatory mortality was then calculated as the difference between total mortality rate and predatory mortality rate.

2.4. Statistics

Normality was tested by the Kolmogorov-Smirnov test (Zar 1984). When necessary, the data were log transformed (n+1) to meet the requirement of a normal distribution. Seasonal and annual differences in the oceanographic conditions, differences in stage duration and predatory and non-predatory mortality rates among development stages and between years were tested with a 2-factor general linear model (α = 0.05) after checking that the data met the parametric assumptions. Spearman rank correlations were used to test for linear relationships between parameters (α = 0.05). Statistical analysis was done using Minitab v. 11.

3. RESULTS

3.1. General oceanographic conditions

Oceanographic conditions for both years are summarized in Table S2. Ekman transport was positive during much of the study period, indicating prevailing upwelling conditions (Fig. 2a). Contrary to a previous suggestion of weak seasonality of upwelling in Mejillones Bay (Sobarzo et al. 2007), we observed significant seasonal variations in Ekman transport (Table S4), with the strongest Ekman transport occurring in late winter and early spring, reaching 700 m^3 s^{-1} km^{-1} in October 2010 and 941 m^3 s^{-1} km^{-1} in September 2011, whereas the lowest values were found in the fall. Water column temperature ranged between 11.9 and 17.3°C during the sampling period, with a warmer period in the summer/fall and a colder period of winter/spring months (Fig. 2b). The water column was strongly thermally stratified, with the isotherm of 16°C at 10 m depth most of the time. The lowest temperatures were recorded in water deeper than 50 m. Intrusion of cold upwelled water caused the shoaling of the 14°C isotherm to near 20 m between July 2010 and March 2011

and in September 2011. Salinity was rather stable at 34.8–34.9 in both years (Fig. 2c) and without significant changes between seasons (Table S4). DO concentration showed similar seasonal patterns between years, with an oxycline at 10–20 m depth (Fig. 2d). In 2010, the average upper boundary of the OMZ (1 ml O$_2$ l^{-1}) was at 22.0 ± 8.8 m, and a very deep OMZ was observed in August. In 2011, the upper limit of the OMZ was at an average depth of
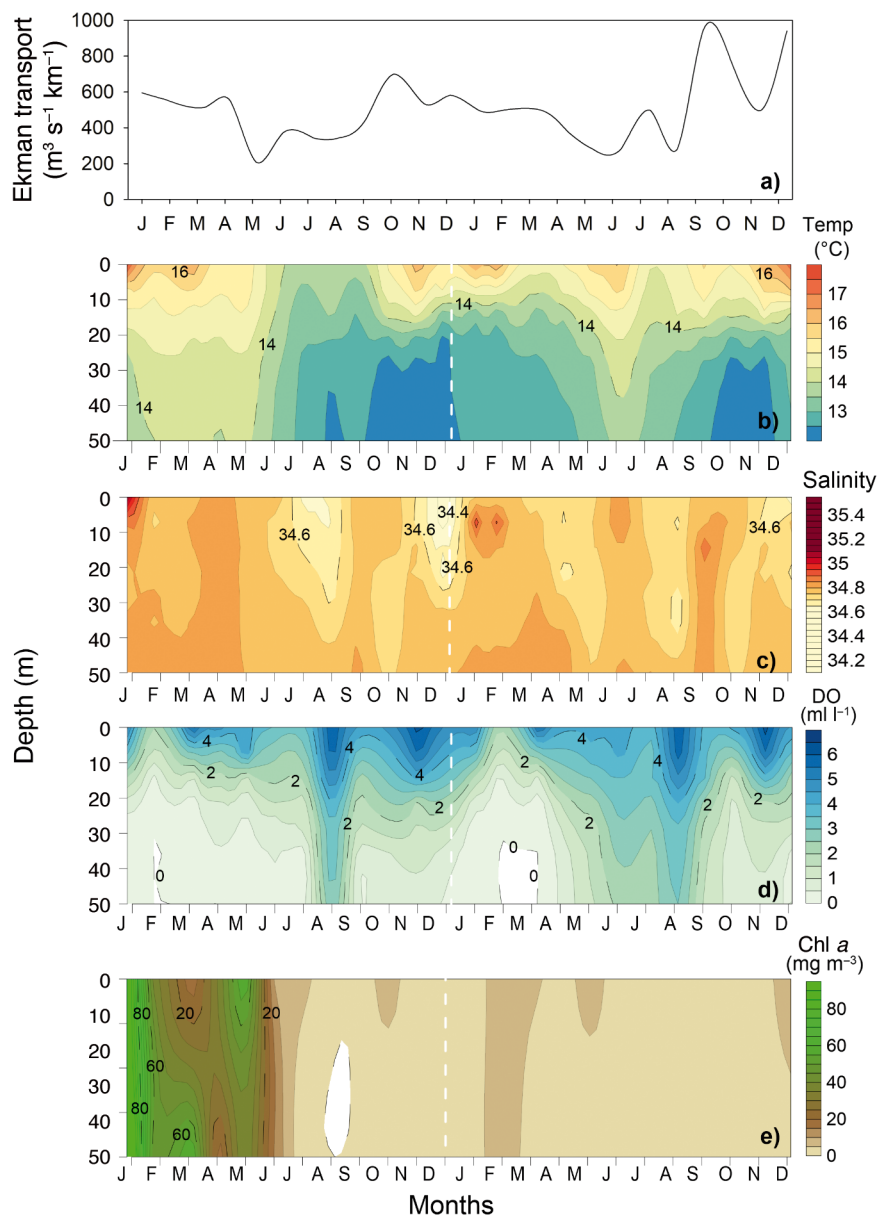

Fig. 2. Oceanographic conditions (average of samples from 3 stations): (a) upwelling index expressed as Ekman transport, (b) temperature, (c) salinity, (d) dissolved oxygen (DO) and (e) phytoplankton biomass, measured as chl a, in Mejillones Bay (northern Chile) during 2010–2011. The white dashed line represents the change between years of sampling. Black dashed lines represent the isolines

26.0 ± 17.0 m and was deeper than in the previous year between June and September. Chl *a* concentrations showed significant seasonal and yearly differences (Fig. 2e, Table S4).

3.2. Predatory and non-predatory mortality rates

There were significant ontogenetic and temporal differences in predatory mortality rate among the 3 copepod species (Table S5). The estimated predatory mortality rate of *Paracalanus* cf. *indicus* was generally higher in the older stages of C3–C5 than in the younger stages of C1–C2 in both years (Fig. 3a,b). The predatory mortality rate of *Acartia tonsa* reached its highest value in C2–C5, especially in the winter–spring period (September–December) in both years, and lowest in the summer period (January–March) (Fig. 3c,d). Likewise, the predatory mortality rate of *Calanus chilensis* was lowest in the summer and fall, and was very high in stages C2–C5, especially in

November (Fg.g 3e,f). Predatory mortality was positively correlated with DO for all 3 species, negatively with chl *a* for *A. tonsa* and negatively with temperature for *C. chilensis* (Table 1).

There were significant ontogenetic, but not temporal, differences in the non-predatory mortality rate of *P.* cf. *indicus* and *C. chilensis*, and the rate also varied significantly between months in *A. tonsa* (Table S5). The estimated non-predatory mortality rate of *P.* cf. *indicus* was generally higher in stage C5 in 2011 and lower in C1–C2 in both years (Fig. 4a,b). The non-predatory mortality rate of *A. tonsa* was highest in C1–C4 in the spring (September–December) in both years and in C5 in the fall–winter period (April–July) and lowest in the summer period (January–March) (Fig. 4c,d). Likewise, the non-predatory mortality rate of *C. chilensis* was lowest in the summer and was high in the spring, especially for C5 (Fig. 4e,f). Non-predatory mortality was significantly and negatively correlated with DO and chl *a* in both *P.* cf. *indicus* and *A. tonsa*,
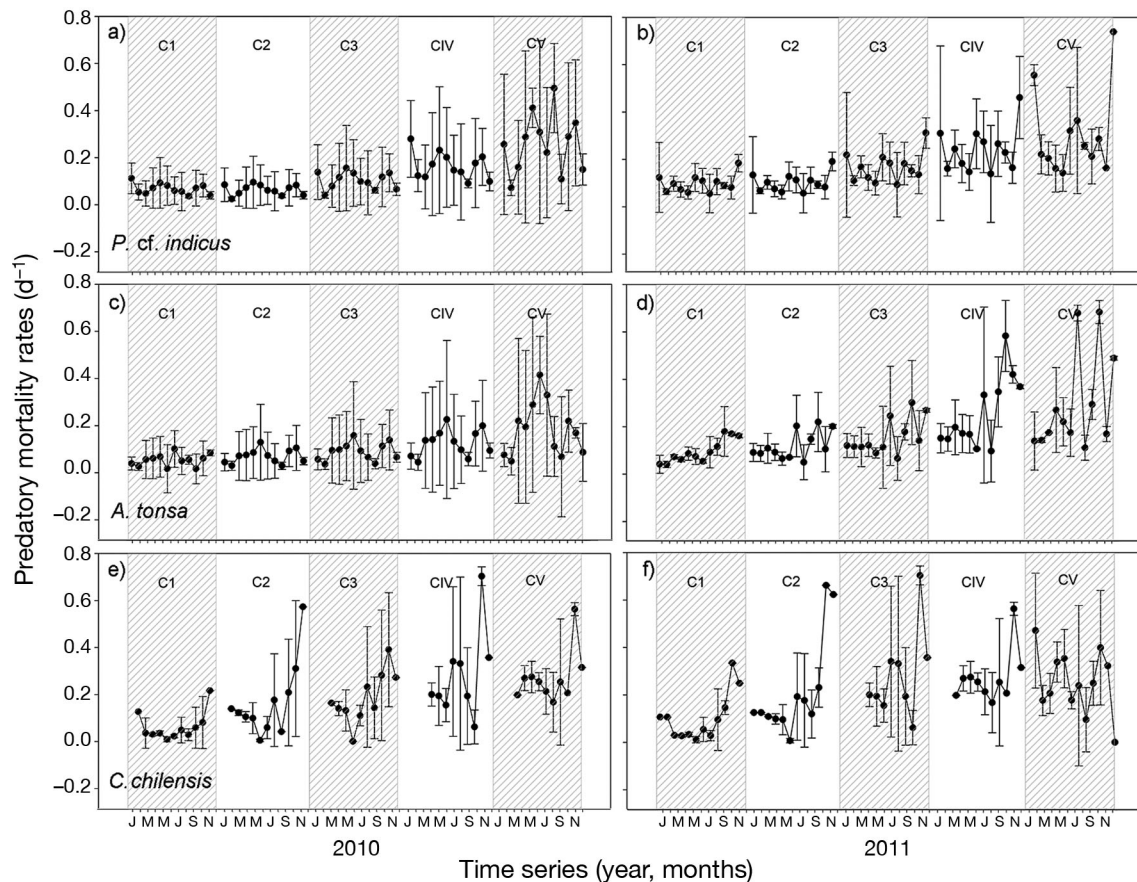

Fig. 3. Monthly predatory mortality rates (mean ± SD) of the 3 dominant copepod species in the HCL in 2010 and 2011 at Mejillones Bay, Chile, according to developmental stage: (a,b) *Paracalanus* cf. *indicus*, (c,d) *Acartia tonsa*, (e,f) *Calanus chilensis*. Months without data points mean the species was absent in those samples

Fig. 4. Monthly non-predatory mortality rates (mean ± SD) of the 3 dominant copepod species in HCL in 2010 and 2011 at Mejillones Bay, Chile, according to developmental stage: (a,b) *Paracalanus* cf. *indicus*, (c,d) *Acartia tonsa*, (e,f) *Calanus chilensis*. Months without data points mean the species was absent in those samples
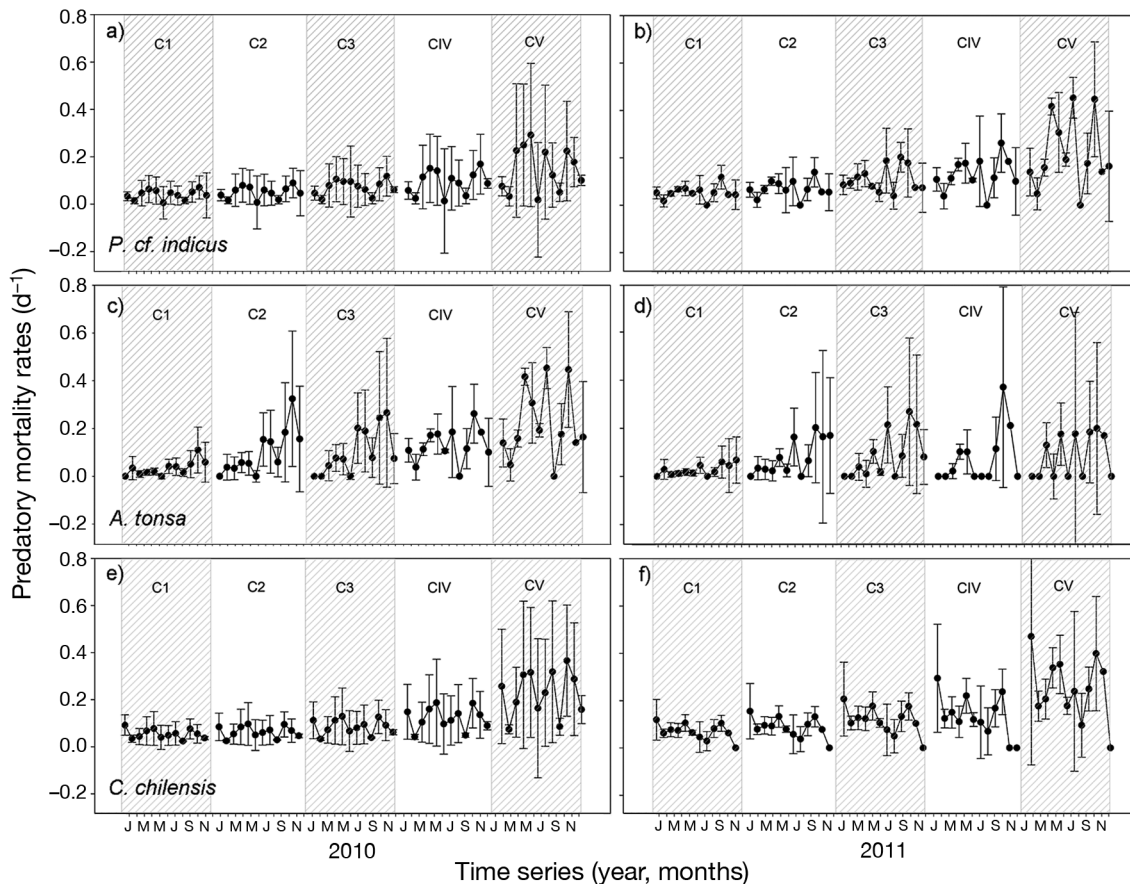
whereas it was positively correlated with temperature in *C. chilensis* (Table 1).

Total mortality rates over the 2 years increased with developmental stages in all 3 species (Table 2, Fig. 5). The partition of mortality between predatory and non-predatory sources, however, remained rather constant across the developmental stages for each species, with predation contributing to a larger portion of the total mortality. On average, predation accounted for 53.7% of the total mortality in *P.* cf.

Table 1. Results of Spearman rank order correlations of predatory and non-predatory mortality rates (d^{-1}) of the 3 dominant copepod species at Mejillones Bay, Chile, with oceanographic variables: temperature (T), salinity (S), dissolved oxygen (DO) and chl *a*. *Significant correlation at $p < 0.05$

Species		Predatory mortality rates				Non-predatory mortality rates			
		T	S	DO	Chl *a*	T	S	DO	Chl *a*
Paracalanus cf. *indicus*	R	0.117	0.143	0.236	−0.099	−0.083	0.317	−0.596	−0.374
	p	0.202	0.120	0.009*	0.291	0.117	0.117	0.000*	0.000*
	n	72	72	72	72	71	71	71	71
Acartia tonsa	R	0.132	0.074	0.352	−0.226	0.022	0.065	−0.574	−0.175
	p	0.151	0.420	0.006*	0.013*	0.676	0.219	0.000*	0.001*
	n	71	71	71	71	72	72	72	72
Calanus chilensis	r	−0.290	−0.102	0.127	0.127	0.532	0.077	0.112	−0.161
	p	0.001*	0.269	0.165	0.058	0.002*	0.143	0.702	0.102
	n	69	69	69	69	71	71	71	71

Table 2. Average prosome length (µm), stage-specific total mortality rate (d^{-1}) and its partition between predatory (PM) and non-predatory (NPM) sources of mortality (%) of the 3 dominant copepod species at Mejillones Bay, Chile

Stage	_Paracalanus_ cf. _indicus_				_Acartia tonsa_				_Calanus chilensis_			
	Prosome length	Total mortality	% PM	% NPM	Prosome length	Total mortality	% PM	% NPM	Prosome length	Total mortality	% PM	% NPM
C1	350.0	0.15	53.3	46.7	528.0	0.15	60.0	40.0	940.0	0.11	63.6	36.4
C2	426.7	0.18	55.6	44.4	596.7	0.17	58.8	41.2	1126.0	0.29	69.0	31.0
C3	592.6	0.24	54.2	45.8	657.9	0.22	54.5	45.5	1278.3	0.32	68.8	31.2
C4	724.7	0.35	54.3	45.7	730.0	0.32	56.3	43.7	1491.7	0.42	66.7	33.3
C5	844.0	0.55	50.9	49.1	870.4	0.46	52.2	47.8	1812.0	0.45	57.8	42.2
		Mean	53.7	46.3		Mean	56.4	43.6		Mean	65.2	34.8

indicus, 56.4% in _A. tonsa_ and up to 65.2% in _C. chilensis_ (Table 2, Fig. 5).

4. DISCUSSION

The high variability of copepod abundances within the HCS (Hidalgo et al. 2010, 2012, Pino-Pinuer 2014, Yáñez et al. 2018) suggests a very dynamic balance between birth and mortality. In addition to predation, the presence of the OMZ and upwelling events are also key drivers of population dynamics and secondary production within the HCS (Escribano et al. 2009, 2012, Yáñez et al. 2012). During this study, the chl _a_ concentration was variable, but it was generally at levels not considered to be limiting to zooplankton (Escribano et al. 2016), except in the winter months, when the water column was more mixed, and the OMZ was restricted to the deeper depths and when chl _a_ was nearly depleted (0.02 mg m^{-3}). The water column was thermally stratified with low DO for much of the year, consistent with previous findings (Escribano et al. 2004, Ruz et al. 2015, 2017).

An interesting observation from this study is that mortality rate increased with developmental stage in all 3 species. Elliott & Tang (2011) showed that over an annual cycle in the Chesapeake Bay (USA), copepodite mortality rates were generally higher than naupliar mortality rates. In Lurefjorden, Norway, where predatory copepods were abundant, the mortality rate of _Calanus_ spp. decreased substantially as the copepods developed through the naupliar stages, but subsequently increased slightly between C1 and C5 (Eiane et al. 2002). A similar increase in mortality rate in late copepodite stages was also observed in _C. finmarchicus_ in the North Sea (Eiane & Ohman 2004).

In our study, we observed that the older copepod stages had a longer stage duration than the earlier stages (Fig. S1), which agrees with an earlier study (Escribano et al. 1998). An increasing stage duration would result in an increasing chance for the older stages to succumb to both predatory and non-predatory mortalities. The estimated mortality rates of C1 were comparable to the global average values (ca. 0.10–0.15 d^{-1}; Hirst & Kiørboe 2002) for the observed temperature range, but were much higher for the later stages (up to 0.55 d^{-1}). Nevertheless, similarly high C5-adult mortality rates have been reported elsewhere; for example, a mortality of ca. 0.5 d^{-1} was reported by Ohman & Hsieh (2008) for _C. pacificus_ within the California coastal upwelling system and by Maud et al. (2018) for _C. helgolandicus_ in the western English Channel. Elliott & Tang (2011) derived temperature-dependent copepodite mortality for _Acartia tonsa_ in the Chesapeake Bay, reaching ca. 0.5 d^{-1} at 14°C, which is nearly the same as our estimate for that average water temperature.
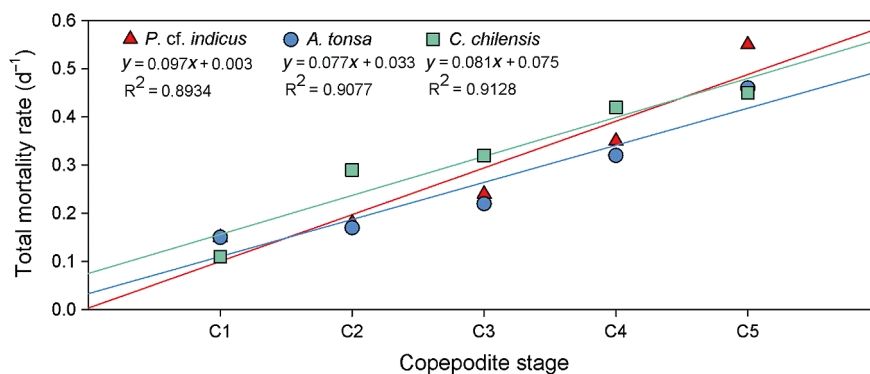

Fig. 5. Total mortality rate as a function of copepodite stages for the 3 dominant copepod species (_Paracalanus_ cf. _indicus_, _Acartia tonsa_, _Calanus chilensis_) in Mejillones Bay, Chile. Lines are linear regression functions fitted at p < 0.05

Apparently, these copepod species have different strategies to maintain their populations despite the high mortality rates. The spawning frequency of these species is unknown, but is probably high because all life stages can be found year-round (Escribano et al. 2007, Hidalgo & Escribano 2008, Ruz et al. 2015), indicating frequent reproduction and short life cycles. A fast development rate may allow early stages to reach maturity sooner, thereby ensuring a continuous supply of gravid females. For example, *C. chilensis* development time is 22 d at 17°C (Escribano et al. 1998), with 17 generations yr^{-1}; *Paracalanus* cf. *indicus* development is 8 d at 17°C, with 45 generations yr^{-1} (Escribano et al. 2014), while *Acartia tonsa* is 25 d at 17°C (McLaren et al. 1969), with 15 generations yr^{-1}. Moreover, *C. chilensis* has a high egg production rate (29 eggs $female^{-1}$ d^{-1}; Escribano et al. 2014), whereas *P.* cf. *indicus* and *A. tonsa* have high egg hatching success (52 and 73%, respectively; Escribano et al. 2014, Ruz et al. 2015). Therefore, rapid development coupled with high hatching success in *P.* cf. *indicus* and *A. tonsa* and a high egg production rate in *C. chilensis* appear to be their strategies for sustaining their populations and achieving dominance in the HCS.

Using neutral red staining and the modified VLT method, we were able to partition mortality into predatory and non-predatory sources. Predatory mortality rates of all 3 species increased linearly with developmental stages hence body size. Larger body size may make the copepodites more conspicuous to visual predators such as planktivorous fish, which often prefer the larger prey (Brooks 1968, O'Brien et al. 1976). Within the HCS, the major planktivores in the oxygenated layer include sardines and anchovies (Espinoza & Bertrand 2008), which may explain the observed positive relationship between predatory mortality rates and copepodite stage (i.e. body size) as well as between predatory mortality rates and DO for 2 of the 3 species.

Intermittent intrusion of oxygen-poor water associated with coastal upwelling is a common feature in the region (Marín et al. 1993), which could cause episodic hypoxia and copepod mortality (Elliott et al. 2010, 2013, Yáñez et al. 2012). In our study, low DO was associated with high non-predatory mortality rates of *P.* cf. *indicus* and *A. tonsa*, consistent with earlier reports (Yáñez et al. 2012, Ruz et al. 2015). In contrast, low DO did not have a significant effect on *C. chilensis*, reflecting the latter species' better ability to cope with a low-oxygen environment (Hirche et al. 2014, Ruz et al. 2018).

Non-predatory mortality rates of *P.* cf. *indicus* and *A. tonsa* were negatively correlated with chl *a* concentration, implying direct or indirect food limitation effects. Interestingly, temperature correlated positively with non-predatory mortality rate but negatively with predatory mortality rate of *C. chilensis*. This species is endemic to the coastal upwelling system (Escribano & Rodriguez 1994, 1995, Escribano 1998). Increasing water column temperature reflects the weakening of the upwelling condition, which may lead to a less favorable living condition and hence a higher non-predatory mortality rate. Meanwhile, a less stratified condition may allow the copepods to migrate deeper diurnally to avoid predation (Hidalgo et al. 2005), resulting in a lower predatory mortality rate.

Overall, the relative proportions of predatory vs. non-predatory mortality rates remained fairly consistent across developmental stages within a species. On average, non-predatory mortality accounted for 34.8–46.3% of the total mortality. This highlights the importance of non-predatory factors such as environmental stresses in driving copepod population dynamics within the HCS (Escribano et al. 2012, Pino-Pinuer et al. 2014, Medellín-Mora et al. 2016).

5. CONCLUSIONS

We investigated copepod mortality rates within the HCS and examined the relative importance of predatory and non-predatory mortalities in relation to environmental conditions. In the Southwest Pacific, climate change is expected to intensify upwelling in the HCS (Echevin et al. 2012). In such a scenario, stronger upwelling may promote extreme shoaling of the OMZ, which compresses the habitat range for zooplankton (Manríquez et al. 2009) and which will likely alter the extent and patterns of both predatory and non-predatory mortality rates of the copepod populations. It is therefore pertinent that researchers consider both mortality sources in order to fully understand copepod population dynamics within this important ecosystem.

LITERATURE CITED

Anabalón V, Arísteguia J, Morales CE, Andrade I and others (2014) The structure of planktonic communities under variable coastal upwelling conditions off Cape Ghir (31°N) in the Canary Current System (NW Africa). Prog Oceanogr 120:320–339

Bělehrádek J (1935) Temperature and living matter. Protoplasma Monogr Vol 8. Gebrüder Borntraeger, Berlin

Bickel S, Tang K (2010) Microbial decomposition of proteins and lipids in copepod versus rotifer carcasses. Mar Biol 157:1613–1624

Bickel SL, Hammond JDM, Tang KW (2011) Boat-generated turbulence as a potential source of mortality among copepods. J Exp Mar Biol Ecol 401:105–109

Brooks LJ (1968) The effects of prey size selection by lake planktivores. Syst Biol 17:273–291

Burns CW (1985) Fungal parasitism in a copepod population: the effects of *Aphanomyces* on the population dynamics of *Boeckella dilatata* Sars. J Plankton Res 7: 201–205

Ceballos S, Kiørboe T (2011) Senescence and sexual selection in a pelagic copepod. PLOS ONE 6:e18870

Delgado M, Alcaraz M (1999) Interactions between red tide microalgae and herbivorous zooplankton: the noxious effects of *Gyrodinium corsicum* (Dinophyceae) on *Acartia grani* (Copepoda: Calanoida). J Plankton Res 21: 2361–2371

Donoso K, Escribano R (2014) Mass-specific respiration of mesozooplankton and its role in the maintenance of an oxygen-deficient ecological barrier (BEDOX) in the upwelling zone off Chile upon presence of a shallow oxygen minimum zone. J Mar Syst 129:166–177

Echevin V, Goubanova K, Belmadani A, Dewitte B (2012) Sensitivity of the Humboldt Current system to global warming: a downscaling experiment of the IPSL-CM4 model. Clim Dyn 38:761–774

Eiane K, Ohman MD (2004) Stage-specific mortality of *Calanus finmarchicus, Pseudocalanus elongatus* and *Oithona similis* on Fladen Ground, North Sea, during a spring bloom. Mar Ecol Prog Ser 268:183–193

Eiane K, Aksnes DL, Ohman MD, Wood S, Martinussen MB (2002) Stage-specific mortality of *Calanus* spp. under different predation regimes. Limnol Oceanogr 47:636–645

Elliott DT, Tang KW (2009) Simple staining method for differentiating live and dead marine zooplankton in field samples. Limnol Oceanogr Methods 7:585–594

Elliott DT, Tang KW (2011) Influence of carcass abundance on estimates of mortality and assessment of population dynamics in *Acartia tonsa.* Mar Ecol Prog Ser 427:1–12

Elliott DT, Harris CK, Tang KW (2010) Dead in the water: the fate of copepod carcasses in the York River estuary, Virginia. Limnol Oceanogr 55:1821–1834

Elliott DT, Pierson JJ, Roman M (2013) Copepods and hypoxia in Chesapeake Bay: abundance, vertical position and non-predatory mortality. J Plankton Res 35:1027–1034

Escribano R (1998) Population dynamics of *Calanus chilensis* in the Chilean Eastern Boundary Humboldt Current. Fish Oceanogr 7:245–251

Escribano R, Rodriguez L (1994) Life cycle of *Calanus chilensis* Brodsky in northern Chile. In: Ferrari FD, Bradley BP (eds) Ecology and morphology of copepods. Kluwer Academic Publishers, Boston, MA, p 289–294

Escribano R, Rodriguez L (1995) Seasonal size variation and growth of *Calanus chilensis* Brodsky in northern Chile. Rev Chil Hist Nat 68:373–382

Escribano R, Rodríguez L, Iribarren C (1998) Temperature-dependent development and growth of *Calanus chilensis* Brodsky from Northern Chile. J Exp Mar Biol Ecol 229: 19–34

Escribano R, Daneri G, Farías L, Gallardo VA and others (2004) Biological and chemical consequences of the 1997–1998 El Niño in the Chilean coastal upwelling system: a synthesis. Deep Sea Res II 51:2389–2411

Escribano R, Hidalgo P, González H, Giesecke R, Riquelme-Bugueño R, Manríquez K (2007) Seasonal and interannual variation of mesozooplankton in the coastal upwelling zone off central-southern Chile. Prog Oceanogr 75:470–485

Escribano R, Hidalgo P, Krautz C (2009) Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000. Deep Sea Res II 56:1083–1094

Escribano R, Hidalgo P, Fuentes M, Donoso K (2012) Zooplankton time series in the coastal zone off Chile: variation in upwelling and responses of the copepod community. Prog Oceanogr 97:174–186

Escribano R, Hidalgo P, Valdés V, Frederick L (2014) Temperature effects on development and reproduction of copepods in the Humboldt Current: the advantage of rapid growth. J Plankton Res 36:104–116

Escribano R, Bustos E, Hidalgo P, Morales CE (2016) Non-limiting food conditions for growth and production of the copepod community in a highly productive upwelling zone. Cont Shelf Res 126:17–14

Espinoza P, Bertrand A (2008) Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current system. Prog Oceanogr 79:215–227

Giraldo A, Escribano R, Marin V (2002) Spatial distribution of *Calanus chilensis* off Mejillones Peninsula (northern Chile): ecological consequences upon coastal upwelling. Mar Ecol Prog Ser 230:225–234

Hidalgo P, Escribano R (2001) Succession of pelagic copepod species in coastal waters off northern Chile: the influence of the 1997–98 El Niño. Hydrobiologia 453: 153–160

Hidalgo P, Escribano R (2008) The life cycles of two co-existing copepods, *Calanus chilensis* and *Centropages brachiatus*, in the upwelling zone off northern Chile (23°S). Mar Biol 155:429–442

Hidalgo P, Escribano R, Morales CE (2005) Ontogenetic vertical distribution and diel migration of the copepod *Eucalanus inermis* in the oxygen minimum zone off northern Chile. J Plankton Res 27:519–529

Hidalgo P, Escribano R, Vergara O, Jorquera E, Donoso K, Mendoza P (2010) Patterns of copepod diversity in the Chilean coastal upwelling system. Deep Sea Res II 57: 2089–2097

Hidalgo P, Escribano R, Fuentes M, Jorquera E, Vergara O (2012) How coastal upwelling influences spatial pat-

terns of size-structured diversity of copepods off cen-tral-southern Chile (summer 2009). Prog Oceanogr 92–95:134–145

Hirche HJ, Barz K, Ayon P, Schulz J (2014) High resolution vertical distribution of the copepod *Calanus chilensis* in relation to the shallow oxygen minimum zone off north-ern Peru using LOKI, a new plankton image system. Deep Sea Res I 88:63–73

Hirst AG, Kiørboe T (2002) Mortality of marine planktonic copepods: global rates and patterns. Mar Ecol Prog Ser 230:195–209

Ivory JA, Tang KW, Takahashi K (2014) Use of Neutral Red in short-term sediment traps to distinguish between zoo-plankton swimmers and carcasses. Mar Ecol Prog Ser 505:107–117

Kimmerer WJ, McKinnon AD (1990) High mortality in a copepod population caused by a parasitic dinoflagellate. Mar Biol 107:449–452

Mann KH, Lazier JNR (1991) Dynamics of marine ecosys-tems: biological-physical interactions in the oceans. Blackwell Scientific Publications, Oxford

Manríquez K, Escribano R, Hidalgo P (2009) The influence of coastal upwelling on the mesozooplankton community structure in the coastal zone off Central/Southern Chile as assessed by automated image analysis. J Plankton Res 31:1075–1088

Marín V, Olivares G (1999) Estacionalidad de la productivi-dad primaria en Bahía Mejillones del Sur (Chile): una aproximación proceso-funcional. Rev Chil Hist Nat 72: 629–641

Marín V, Rodríguez L, Vallejo L, Fuenteseca J, Oyarce E (1993) Efectos de la surgencia costera sobre la produc-tividad primaria primavera de la Bahía Mejillones de Sur (Antofagasta, Chile). Rev Chil Hist Nat 66:479–491

Maud J, Hirst AG, Atkinson A, Lindeque PK, McEvoy AJ (2018) Mortality of *Calanus helgolandicus*: sources, dif-ferences between the sexes and consumptive and non consumptive processes. Limnol Oceanogr 63:1741–1761

McLaren IA, Corkett CJ, Zillioux EJ (1969) Temperature adaptations of copepod eggs from the Artic to the tropics. Biol Bull (Woods Hole) 137:486–493

Medellín-Mora J, Escribano R, Schneider W (2016) Commu-nity response of zooplankton to oceanographic changes (2002–2012) in the central/southern upwelling system of Chile. Prog Oceanogr 142:17–29

Morales CE, Anabalón V (2012) Phytoplankton biomass and microbial abundances during the spring upwelling sea-son in the coastal area off Concepción, central-southern Chile: variability around a time series station. Prog Oceanogr 92–95:81–91

O'Brien WJ, Slade NA, Vinyard GL (1976) Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57:1304–1310

Ohman MD, Hsieh CH (2008) Spatial differences in mortal-ity of *Calanus pacificus* within the California Current System. J Plankton Res 30:359–366

Ohman MD, Wood SN (1995) The inevitability of mortality. ICES J Mar Sci 52:517–522

Ohtsuka S, Hora M, Suzaki T, Arikawa M, Omura G, Yamada K (2004) Morphology and host-specificity of the apostome ciliate *Vampyrophrya pelagica* infecting pe-lagic copepods in the Seto Inland Sea, Japan. Mar Ecol Prog Ser 282:129–142

Pino-Pinuer P, Escribano R, Hidalgo P, Riquelme-Bugueño R, Schneider W (2014) Copepod community response to

variable upwelling conditions off central-southern Chile during 2002–2004 and 2010–2012. Mar Ecol Prog Ser 515:83–95

Roman MR, Gauzens AL, Rhinehart WK, White JR (1993) Effects of low oxygen waters on Chesapeake Bay zoo-plankton. Limnol Oceanogr 38:1603–1614

Runge JA, Franks PJS, Gentleman WC, Megrey BA, Rose KA, Werner FE, Zakardjian B (2004) Diagnosis and pre-diction of variability in secondary production and fish recruitment processes: developments in physical-biolog-ical modeling. In: Robinson AR, Brink KH (eds) The sea, Vol 13. Harvard University Press, Cambridge, MA, p 413–473

Ruz PM, Hidalgo P, Yáñez S, Escribano R, Keister JE (2015) Egg production and hatching success of *Calanus chilen-sis* and *Acartia tonsa* in the northern Chile upwelling zone (23°S), Humboldt Current System. J Mar Syst 148: 200–212

Ruz PM, Hidalgo P, Riquelme-Bugueño R, Franco-Cisterna B, Cornejo M (2017) Vertical distribution of copepod eggs in the oxygen minimum zone off Mejillones Bay (23°S) in the Humboldt Current System. Mar Ecol Prog Ser 571:83–96

Ruz PM, Hidalgo P, Escribano R, Keister JE, Yebra L, Franco-Cisterna B (2018) Hypoxia effects on females and early stages of *Calanus chilensis* in the Humboldt Current ecosystem (23°S). J Exp Mar Biol Ecol 498: 61–71

Saiz E, Calbet A, Grifell K, Bersano JGF and others (2015) Ageing and caloric restriction in a marine planktonic copepod. Sci Rep 5:14962

Sampei M, Sasaki H, Hattori H, Forest A, Fortier L (2009) Significant contribution of passively sinking copepods to the downward export flux in Arctic waters. Limnol Oceanogr 54:1894–1900

Sampei M, Sasaki H, Forest A, Fortier L (2012) A substantial export flux of particulate organic carbon linked to sink-ing dead copepods during winter 2007-2008 in the Amundsen Gulf (southeastern Beaufort Sea, Arctic Ocean). Limnol Oceanogr 57:90–96

Sobarzo M, Bravo L, Donoso D, Garcés-Vargas J, Schneider W (2007) Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile. Prog Oceanogr 75:373–382

Tang KW, Freund CS, Schweitzer CL (2006) Occurrence of copepod carcasses in the lower Chesapeake Bay and their decomposition by ambient microbes. Estuar Coast Shelf Sci 68:499–508

Tang KW, Bickel SL, Dziallas C, Grossart HP (2009) Micro-bial activities accompanying decomposition of clado-ceran and copepod carcasses under different environ-mental conditions. Aquat Microb Ecol 57:89–100

Tang KW, Gladyshev MI, Dubovskaya OP, Kirillin G, Grossart HP (2014) Zooplankton carcasses and non-predatory mortality in freshwater and inland sea envi-ronments. J Plankton Res 36:597–612

Tang KW, Blackhaus LV, Riemann L, Koski M, Grossart HP, Munk P, Nielsen TG (2019a) Copepod carcasses in the Subtropical Convergence Zone of the Sargasso Sea: implications for microbial community composition, sys-tem metabolism and carbon flux. J Plankton Res 41: 549–560

Tang KW, Ivory JA, Shimode S, Nishibe Y, Takahashi K (2019b) Dead heat: copepod carcass occurrence along the Japanese coasts and implications for a warming

ocean. ICES J Mar Sci, doi.org/10.1093/icesjms/fsz017

Thiel M, Macaya EC, Acuña E, Arntz WE and others (2007) The Humboldt Current System of Northern and Central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. Oceanogr Mar Biol Annu Rev 45:195–344

Tsuda A (1994) Starvation tolerance of a planktonic marine copepod *Pseudocalanus newmani* Frost. J Exp Mar Biol Ecol 181:81–89

Verity PG, Smetacek V (1996) Organism life cycles, predation, and the structure ofmarine pelagic ecosystems. Mar Ecol Prog Ser 130:277–293

Yáñez S (2009) Tasa de mortalidad y desarrollo de Paracalanus cf. indicus (Copepoda:Calanoida) (Wolfender,

1905) en la zona Centro-Sur de Chile (36S) asociada con la zona de mínimo de oxígeno. PhD dissertation, Universidad de Concepción

Yáñez S, Hidalgo P, Escribano R (2012) Natural mortality of *Paracalanus indicus* (Copepoda: Calanoida) in coastal upwelling areas associated with oxygen minimum zone in the Humboldt current system: implications for the passive carbon flux. Rev Biol Mar Oceanogr 47:295–310

Yáñez S, Hidalgo P, Ruz P, Tang K (2018) Copepod secondary production in the sea: errors due to uneven molting and growth patterns and incidence of carcasses. Prog Oceanogr 165:257–267

Zar JH (1984) Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ