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KW Tang

Virginia Institute of Marine Science

MI Gladyshev

OP Dubovskaya

G Kirillin

HP Grossart

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REVIEW

Zooplankton carcasses and non-predatory mortality in freshwater and inland sea environments

KAM W. TANG^{1,2*}, MICHAEL I. GLADYSHEV^{3,4}, OLGO P. DUBOVSKAYA^{3,4}, GEORGIY KIRILLIN⁵ AND HANS-PETER GROSSART^{6,7}

¹VIRGINIA INSTITUTE OF MARINE SCIENCE, COLLEGE OF WILLIAM & MARY, GLOUCESTER POINT, VA, USA, ²DEPARTMENT OF BIOSCIENCES, SWANSEA UNIVERSITY, SWANSEA, WALES SA2 8PP, UK, ³INSTITUTE OF BIOPHYSICS OF SIBERIAN BRANCH OF THE RUSSIAN ACADEMY OF SCIENCE, AKADEMGORODOK, KRASNOYARSK 660036, RUSSIA, ⁴SIBERIAN FEDERAL UNIVERSITY, SVOBODNY AV. 79, KRASNOYARSK 660041, RUSSIA, ⁵DEPARTMENT OF ECOHYDROLOGY, LEIBNIZ-INSTITUTE OF FRESHWATER ECOLOGY AND INLAND FISHERIES, MÜGGELSEEDAMM 310, BERLIN 12587, GERMANY, ⁶DEPARTMENT OF EXPERIMENTAL LIMNOLOGY, LEIBNIZ-INSTITUTE OF FRESHWATER ECOLOGY AND INLAND FISHERIES, ALTE FISCHERHÜTTE 2, STECHLIN 16775, GERMANY AND ⁷INSTITUTE FOR BIOCHEMISTRY AND BIOLOGY, POTSDAM UNIVERSITY, AM NEUEN PALAIS 10, POTSDAM 14469, GERMANY

*CORRESPONDING AUTHOR: k.wtang@swansea.ac.uk

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Zooplankton carcasses are ubiquitous in marine and freshwater systems, implicating the importance of non-predatory mortality, but both are often overlooked in ecological studies compared with predatory mortality. The development of several microscopic methods allows the distinction between live and dead zooplankton in field samples, and the reported percentages of dead zooplankton average 11.6 (minimum) to 59.8 (maximum) in marine environments, and 7.4 (minimum) to 47.6 (maximum) in fresh and inland waters. Common causes of non-predatory mortality among zooplankton include senescence, temperature change, physical and chemical stresses, parasitism and food-related factors. Carcasses resulting from non-predatory mortality may undergo decomposition leading to an increase in microbial production and a shift in microbial composition in the water column. Alternatively, sinking carcasses may contribute significantly to vertical carbon flux especially outside the phytoplankton growth

seasons, and become a food source for the benthos. Global climate change is already altering freshwater ecosystems on multiple levels, and likely will have significant positive or negative effects on zooplankton non-predatory mortality. Better spatial and temporal studies of zooplankton carcasses and non-predatory mortality rates will improve our understanding of this important but under-appreciated topic.

KEYWORDS: carbon flux; inland waters; lakes; live/dead sorting; non-predatory mortality; zooplankton carcasses

INTRODUCTION

Zooplankton (here referring to mesozooplankton; 200–2000 μm) perform many important ecological functions such as grazing (Calbet, 2001), trophic transfer (Fernando, 1994), nutrient recycling (Vanni, 2002) and involvement in the biological pump (Ducklow et al., 2001). To fully understand the ecological significance of zooplankton, it is necessary to study their life cycle, which can be defined by the basic parameters of reproduction, growth and mortality. Of these, mortality is perhaps the least studied (Runge et al., 2004) and is often assumed to be caused by predation only. In reality, zooplankton also suffer from non-predatory mortality, which may leave nutrient- and carbon-rich carcasses behind. Hirst and Kiørboe (Hirst and Kiørboe, 2002) estimated that non-predatory factors account for 1/4–1/3 of the total mortality among epi-pelagic marine copepods. Ignoring carcasses in field samples therefore will lead to errors in demographic assessment, and

oversight of carcass-mediated nutrient and carbon fluxes as well as microbial processes (Fig. 1).

Tang and Elliott (Tang and Elliott, in press) recently reviewed the occurrence, fate and ecological importance of zooplankton carcasses, but focused mainly on marine copepods and the western literature. Limnologists have long appreciated the occurrence of zooplankton carcasses in lakes and inland waters, and many of the earlier studies were reported in non-English literature, which unfortunately is less accessible to the wider research community. Thus, the purpose of this article is to review the state-of-the-knowledge of zooplankton carcasses and related ecological processes in lakes and inland waters. Some of the concepts and processes discussed are, however, also applicable to the marine environments. We include non-English literature to highlight the work pioneered by Russian scientists on this research topic. Where appropriate, comparison with the marine literature is made.

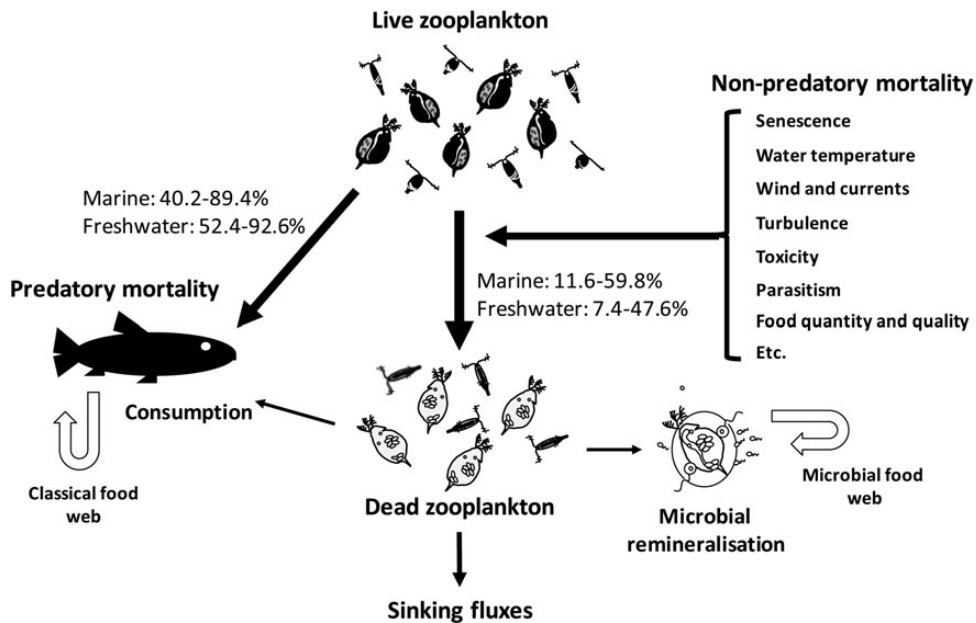


Fig. 1. Based on the literature data, on average 11.6–59.8% of the marine zooplankton and 7.4–47.6% of the freshwater zooplankton are carcasses (Tables II and III), likely the results of non-predatory mortality such as senescence, temperature variations, physical and chemical stresses, parasitism and food-related factors. Carcasses resulting from non-predatory mortality can be incorporated into the classical food web through direct consumption, be incorporated into the microbial food web through microbial decomposition or become part of the sinking fluxes.

METHODS FOR LIVE/DEAD SORTING OF ZOOPLANKTON

Various methods exist for sorting live/dead zooplankton (Table I). Kastalskaja-Karzinkina (Kastalskaja-Karzinkina, 1935, 1937) was the first Russian researcher to study live/dead zooplankton. By staining preserved samples with a 5% solution of erythrosine, dead zooplankton in Glubokoie Lake could be distinguished from live ones based on morphological changes within as little as 3 h after death. This method was later used in the Black Sea (Zelezinskaya, 1966). Alternatively, some researchers examined, without staining, postmortem morphological changes of the zooplankton (Koval, 1984; Geptner *et al.*, 1990; Gruzov *et al.*, 1994; Pavlova and Melnikova, 2006a,b, 2011). Sampei *et al.* (Sampei *et al.*, 2009) collected copepods in the Beaufort Sea and killed them with formalin to simulate death in poisoned sediment traps, or by crowding or heat to simulate death before entering the traps. In the latter treatments, 64% of *Calanus hyperboreus* and *C. glacialis*, and 44% of *Pareuchaeta glacialis* had different appearance of their antennules and swimming legs than those killed by formalin, providing a basis for separating live and dead copepods in sediment trap samples (Sampei *et al.*, 2009, 2012).

Several vital and mortal staining methods have been developed for live/dead sorting. For freshwater zooplankton, a 5–7.5% solution of Aniline Blue ($C_{37}H_{27}N_3O_9S_3Na_2$) has been commonly used based on the protocol originally described by Seepersad and colleagues (Seepersad and Crippen, 1978; Seepersad *et al.*, 2004) and further improved by Bickel *et al.* (Bickel *et al.*, 2009). The zooplankton sample is stained for ca. 15 min, after which it is rinsed to remove excess stain and preserved (e.g. Dubovskaya and Gladyshev, 1983; Telesh, 1986; Dubovskaya, 1987;

Sergeeva *et al.*, 1989). Aniline Blue is classified as a mortal stain; i.e. it penetrates and stains dead zooplankton a bright blue color, whereas live zooplankton do not take up the stain (Dubovskaya, 2008b; Bickel *et al.*, 2009). Live zooplankton that are damaged during sampling and handling give a specific staining pattern different from dead specimens (Supplementary data, Fig. S1).

Another commonly used stain is the vital stain Neutral Red ($C_{15}H_{17}ClN_4$). The basic procedures were described in the 70s (Dressel *et al.*, 1972; Crippen and Perrier, 1974; Fleming and Coughlan, 1978), and an improved protocol is given by Elliott and Tang (Elliott and Tang, 2009). When treated with ca. 0.015 g L^{-1} Neutral Red prior to preservation, live zooplankton are stained bright red whereas dead ones are unstained. This stain is used primarily in marine and estuarine settings (e.g. Vinogradov *et al.*, 1998; Elliott and Tang, 2011a; Litvinyuk *et al.*, 2011). The staining intensity of field samples may vary, in which case digital images can be taken of questionable specimens for more detailed analysis (Litvinyuk and Mukhanov, 2012). Semenova (Semenova, 2010a) compared the use of Aniline Blue and Neutral Red in the brackish Curonian Lagoon, and found the latter often did not stain live Rotifera and Cladocera. Elliott and Tang (Elliott and Tang, 2009) also reported that Neutral Red did not work well in freshwater.

In Lake Baikal, Procion Brilliant Red (H-E3B, reactive red 120) solution (1.25 g L^{-1}) was used to differentiate live/dead copepods in preserved samples (Kozhova, 1991; Riapenko and Polynov, 1991; Naumova, 2006). However, a detailed protocol and its comparison with the other stains have not been published. Fluorescein diacetate (FDA) has been used to assess embryo viability (Buttino *et al.*, 2004) and for live/dead sorting in the

Table I: Published methods for distinguishing between live and dead zooplankton in marine and freshwater samples

Method	Environmental setting	Observations	Key references
Erythrosine staining	Freshwaters	Decay of muscle fibers and integuments become more visible	Kastalskaja-Karzinkina, 1935
Postmortem morphology	Sea waters	Decay of muscle fibers and integuments	Koval, 1984
Postmortem morphology	Sea waters	Changes in morphology and posture of antennules and swimming legs	Sampei <i>et al.</i> , 2009
Aniline Blue staining	Fresh to brackish waters	Dead zooplankton stained blue; live zooplankton do not stain	Seepersad and Crippen, 1978
Neutral Red staining	Sea and estuarine waters	Dead zooplankton do not stain; live zooplankton stained red	Fleming and Coughlan, 1978
Procion Brilliant Red staining	Freshwaters	Dead zooplankton stained red; live zooplankton do not stain	Naumova, 2006
Fluorescein diacetate staining	Sea waters	Live zooplankton show a green fluorescence.	Buttino <i>et al.</i> , 2004
SYTOX Green staining	Sea waters	Dead zooplankton show a green fluorescence	Buttino <i>et al.</i> , 2004
Cell digestion assay		Partial digestion of dead cells, but only for organisms $< 50\ \mu\text{m}$	Zetsche and Meysman, 2012

Descriptions of the original protocols are given in the key references indicated. Examples of application and improvement of some of the methods are given in the text.

Table II: Minimum and maximum percentages of dead zooplankton reported for various marine environments as determined by morphology in unstained samples (U), staining with erythrosine (E), neutral Red (NR) or fluorescein diacetate (FDA)

Location	Method	Taxon	% dead		Reference
			Min.	Max.	
Black Sea, Odessa coast	E	<i>Acartia clausi</i>	1	53	Zelezinskaya, 1966
		<i>Penilia avirostris</i>	16	64	
Atlantic off American Coast	U	Mixed species	50	70	Wheeler, 1967
Atlantic off African Coast	U	Mixed species	16	28	Weikert, 1977
Black Sea, shelf	U	Mixed species	0	100	Koval, 1984
North Atlantic	U	Mixed species	25	50	Roe, 1988
Sea of Japan	U	Mixed species	16	28	Terazaki and Wada, 1988
Red Sea	U	Mixed species	1	50	Böttger-Schnack, 1990
Indian Ocean off African Coast	U	Mixed species	2	100	Geptner <i>et al.</i> , 1990
Baltic Sea, Gotland depression	NR	Mixed species	2	46	Kulikov, 1990
Black Sea, northern part	U	Mixed species	0	100	Gruzov <i>et al.</i> , 1994
Red Sea	U	Mixed species	10	29	Böttger-Schnack, 1995
Gulf of Eilat	U	Mixed species	10	60	Genin <i>et al.</i> , 1995
Pacific near California Bight	U	Mixed species	10	60	Haury <i>et al.</i> , 1995
Arabian Sea	U	Mixed species	5	70	Böttger-Schnack, 1996
Gulf Stream and Labrador Current	NR	Mixed species	0	38	Vinogradov <i>et al.</i> , 1998
North Pacific	U	Mixed species	0	75	Yamaguchi and Ikeda, 2001
North Pacific	U	Mixed species	10	90	Yamaguchi <i>et al.</i> , 2002
Gulf of Aqaba	U	Mixed species	10	20	Yahel <i>et al.</i> , 2005
Chesapeake Bay	NR	Mixed species	13	37	Tang <i>et al.</i> , 2006a
Black Sea, Sevastopol Bay	U	Copepoda	26	51	Pavlova and Melnikova, 2006a
		Cladocera	17	73	
		<i>Noctiluca</i>	14	74	
		Cirripedia larvae	38	68	
		Polychaeta larvae	14	44	
		Mollusca larvae	11	33	
		Mixed species	11	57	
Black Sea, Sevastopol Bay	U	Mixed species	7	60	Pavlova and Melnikova, 2011
Black Sea, Sevastopol Bay	U	Cladocera	20	74	
		Copepoda	13	59	
		Larvae	10	74	
		Mixed species	2	85	
Black Sea, Sevastopol Bay	NR, FDA	Mixed species	2	85	Litvinyuk <i>et al.</i> , 2011
Chesapeake Bay	NR	<i>Acartia tonsa</i>	2	53	Bickel <i>et al.</i> , 2011
Average ± SE			11.6 ± 1.9	59.8 ± 3.7	

Black Sea (Litvinyuk *et al.*, 2009, 2011). The latter authors obtained very similar results with FDA and Neutral Red (Litvinyuk *et al.*, 2011). In a comparison of three methods for live/dead sorting: cell digestion assay, staining with SYTOX[®] Green, and staining with Neutral Red, Neutral Red was by far the best for marine plankton >50 μm (Zetsche and Meysman, 2012).

In summary, Aniline Blue is the most effective for live/dead sorting of fresh and brackish water zooplankton and Neutral Red for marine zooplankton. Both stains are inexpensive and are considered non-hazardous chemicals and therefore particularly suitable for field applications.

ZOOPLANKTON CARCASS DATA FROM THE LITERATURE

In marine environments, high carcass abundances have often been found in polluted areas (Kulikov, 1990; Pavlova

and Melnikova, 2006a,b, 2011) and in deep layers (Geptner *et al.*, 1990; Gruzov *et al.*, 1994; Vinogradov *et al.*, 1998). The minimum percentages of dead marine zooplankton varied from 0 to 50%, with an average of ca. 12% (Table II) and a median of 10%, and were normally distributed (the Kolmogorov–Smirnov test; $D_{K-S} = 0.163$, $P > 0.20$, $n = 33$) (Fig. 2a). The maximum values varied from 20 to 100%, with both mean and median at 60% (Table II), and also were normally distributed ($D_{K-S} = 0.088$, $P > 0.20$, $n = 33$) (Fig. 2b).

In freshwaters, the minimum percentages of dead zooplankton ranged from 0 to 64% with an average of ca. 7% (Table III), close to that for marine zooplankton. However, the set of minimum values had a median of 0.2, significantly lower than that for marine zooplankton (the Mann–Whitney *U*-test, $P = 0.005$, $n = 41$ and 33). The set of minimum values were not normally distributed ($D_{K-S} = 0.292$, $P < 0.01$, $n = 41$) (Fig. 3a). In other words, zero dead zooplankton was more frequently

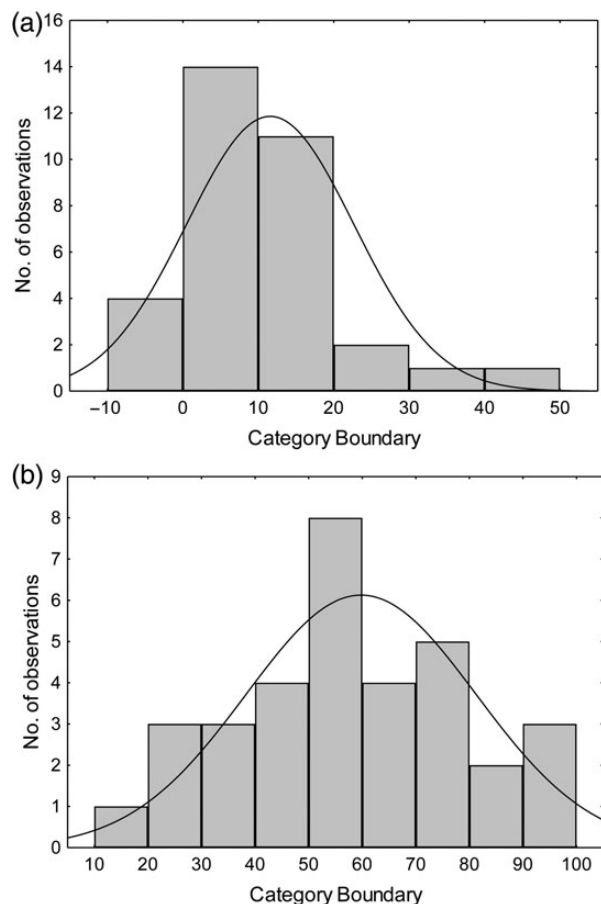


Fig. 2. Frequency distributions of (a) minimum, and (b) maximum percentages of dead zooplankton observed in marine environments. Lines are expected normal distributions for reference.

observed in freshwaters than in the marine environments. The maximum percentages of dead freshwater zooplankton ranged from 2 to 100% with a mean of ca. 48% and a median of 44% (Table III) and were normally distributed ($D_{K-S} = 0.131$, $P > 0.20$, $n = 41$) (Fig. 3b). The maximum values in freshwaters on average did not differ significantly from those in marine environments (Student's t -test, 1.86, $P = 0.067$, $n = 41$ and 33).

In general, the highest percentages of dead freshwater zooplankton (100%) were found in rivers (Dubovskaya, 1987; Gladyshev, 1993; Table III) and in overheated littoral zones (Buseva, 2011; Table III). Comparatively high percentages of carcasses were found in polluted areas (Kozhova, 1991; Gladyshev, 1993; Smelskaya, 1995; Semenova, 2010b) and during cyanobacteria blooms (Semenova, 2011). High carcass abundances were also observed in deep layers of lakes, probably as a result of their sinking from above and/or unfavorable local conditions (Kastalskaja-Karzinkina, 1935; Dubovskaya, 1987).

In summary, the observed percentages of dead zooplankton vary within the whole possible range, 0–100%,

and carcass abundances will be determined by mortality rate and carcass turnover rate at any particular location. A common practice in zooplankton population modeling is to use mortality as the closure term and attribute it only to predation (Edwards and Brindley, 1999). However, Elliott and Tang (Elliott and Tang, 2011b) showed that neglecting even a small degree of non-predatory mortality will lead to unrealistic projections of population growth. Because non-predatory mortality is defined as mortality not due to predation, it has literally unlimited number of possible causes. Nonetheless, we may consider several common causes: senescence, physical and chemical stresses, parasitism and food-related mortality.

PHYSIOLOGICAL DEATH AND ESTIMATION OF NON-PREDATORY MORTALITY

Mortality in the absence of predators can be partly explained by physiological death or senescence. Dorazio (Dorazio, 1984) calculated theoretical curves of mortality under different population growth rates for animals whose only source of mortality is death at some finite age. His calculations showed that senescence mortality becomes more important for slow-growing populations with a short lifespan. He also calculated this mortality for a population growing at 0.1 day^{-1} with different survival curves. For Type I survival curve, physiological death rate is low for juveniles but increases with age, and with a lifespan of 20 days, it accounts for a fraction of 0.38 of the total mortality. Such a high senescence mortality rate has been demonstrated experimentally for *Daphnia* (Hülsmann and Voigt, 2002). For Type II (equal mortality at different ages) and III (high juvenile mortality) survival curves, this fraction drops to 0.21 and 0.07, respectively (Dorazio, 1984).

Romanovsky and Ghilarov (Romanovsky and Ghilarov, 1996) estimated a senescence mortality of 0.045 day^{-1} for *Diaphanosoma brachyurum*. Dodson (Dodson, 1972) assumed the physiological death of *Daphnia rosea* to be 0.03 day^{-1} based on earlier data (Hall, 1964). Romanovsky (Romanovsky, 1984) estimated that the typical lower limits of physiological death rate for zooplankton to be $0.04\text{--}0.06 \text{ day}^{-1}$. The average per day senescence death rate of marine zooplankton of size $> 1.5 \text{ mm}$ is assumed to be 0.05 day^{-1} of the biomass, and for animals of size $< 1.5 \text{ mm}$ it is 0.01 day^{-1} of the biomass (Lebedeva et al., 1982; Sazhin, 1986). Note that only the papers of Lebedeva et al. (Lebedeva et al., 1982) and Sazhin (Sazhin, 1986) derive mortality rates from biomass; all others are based on abundances.

The aforementioned estimations were based on laboratory cultures and modeling, rather than *in situ*

Table III: Minimum and maximum percentages of dead zooplankton reported for various fresh and brackish water environments as determined by morphology in unstained samples (U), staining with erythrosine (E), Aniline Blue (AB) or Procion Brilliant Red (PBR)

Location	Method	Taxon	% dead		Reference
			Min.	Max.	
Glubokoie Lake	E	Rotatoria	31	94	Kastalskaja-Karzinkina, 1935
		Cladocera	64	96	
		Copepoda	35	80	
Glubokoie Lake	E	<i>Daphnia</i>	10	47	Kastalskaja-Karzinkina, 1937
		<i>Bosmina</i>	20	47	
		<i>Diaphanosoma</i>	17	69	
		<i>Eudiaptomus</i>	8	84	
		<i>Mesocyclops</i>	17	37	
		Rotifera	4	93	
		Cladocera	0	20	
Neva River and Lake Ladoga	AB	Copepoda	0	50	Telesh, 1986
		Rotifera	0	40	
		Mixed species	16	96	
Sayano-Shushenskoie Reservoir	AB	Mixed species	0	100	Dubovskaya, 1987
Yenisei River	AB	Mixed species	0	100	Dubovskaya, 1987
Krivorozhskaya Reservoir	AB	Mixed species	0.7	5.5	Sergeeva et al., 1989
Lake Baikal	PBR	<i>Epishura</i>	0	75	Riapenko and Polynov, 1991
Lake Baikal	PBR	<i>Epishura</i>	0	44	Kozhova, 1991
Krasnoyarsk Reservoir	AB	Mixed species	2.5	34	Gladyshev, 1993
Syda River	AB	Mixed species	28.5	100	Gladyshev, 1993
Galichskoie Lake	AB	<i>Mesocyclops</i>	0.17	15	Smelskaya, 1995
Lesnoi pond	AB	<i>Bosmina</i>	0	11.4	Gladyshev and Gubanov, 1996
Lake Constance	U	<i>Cyclops vicinus</i>	0.1	11.5	Gries and Gude, 1999
		<i>Daphnia galeata</i>	0.1	18	
		<i>Daphnia hyalina</i>	0	2	
		Mixed species	0	16.7	
Krasnoyarsk Reservoir	AB	Mixed species	0	22.1	Dubovskaya et al., 2004
Yenisei River	AB	Mixed species	0	22.1	Dubovskaya et al., 2004
Bugach reservoir	AB	<i>Cyclops</i>	0	20.1	Dubovskaya, 2005
		<i>Daphnia</i>	0	46.6	
Lake Baikal	PBR	<i>Epishura</i>	0	80	Naumova, 2006
Obsterno Lake	AB	Mixed species	0.1	6.2	Dubovskaya et al., 2007
Lake Stechlin	AB	<i>Daphnia</i>	0	36.3	Bickel et al., 2009
		<i>Bosmina</i>	0	47.6	
		Copepodites	0	4.6	
		<i>Daphnia</i>	0.4	9.8	
Lake Dagow	AB	<i>Bosmina</i>	1.1	60.8	Bickel et al., 2009
		Copepodites	0	34.4	
		<i>Daphnia</i>	4	100	
		<i>Diaphanosoma</i>	4	100	
Belarus lakes	AB	<i>Daphnia</i>	23	91	Buseva, 2011
		<i>Ceriodaphnia</i>	8	13	
		<i>Bosmina</i>	11	44	
		Mixed species	0.4	47.8	
Curonian Lagoon	AB	Mixed species	0.4	47.8	Semenova, 2011
Average ± SE			7.4 ± 2.1	47.6 ± 5.1	

measurements. A way of measuring *in situ* non-predatory mortality was proposed by Gladyshev and Gubanov (Gladyshev and Gubanov, 1996), and further developed by others (Dubovskaya et al., 1999, 2003; Gladyshev et al., 2003a). The method involves the use of non-poisoned sediment trap and a water column sampler, and applies the following equation:

$$m_i = \frac{\Delta y}{\Delta t_i \cdot N_i} + G_i \cdot \frac{y_i}{N_i} \quad (1)$$

where m_i (day^{-1}) is the specific non-predatory mortality, $\Delta t_i = t_{i+1} - t_i$, with t_i being the instant of taking the sample i , y_i is the abundance of carcasses ($\text{ind.} \cdot \text{m}^{-3}$)

above the trap at time t_i , $\Delta y_i = y_{i+1} - y_i$, and N_i is the abundance of live individuals ($\text{ind.} \cdot \text{m}^{-3}$) above the trap. G_i is the specific removal rate of carcasses from the water column, and is a function of decomposition, consumption and sedimentation. However, sedimentation is assumed to be the principal removal mechanism (Dubovskaya et al., 1999; Dubovskaya, 2008b) such that $G = V/h$, where h is water column thickness (m) above the trap. The sinking velocity of carcasses, V ($\text{m} \cdot \text{day}^{-1}$), is calculated as

$$V = \frac{\gamma}{S \cdot \rho^*} \quad (2)$$

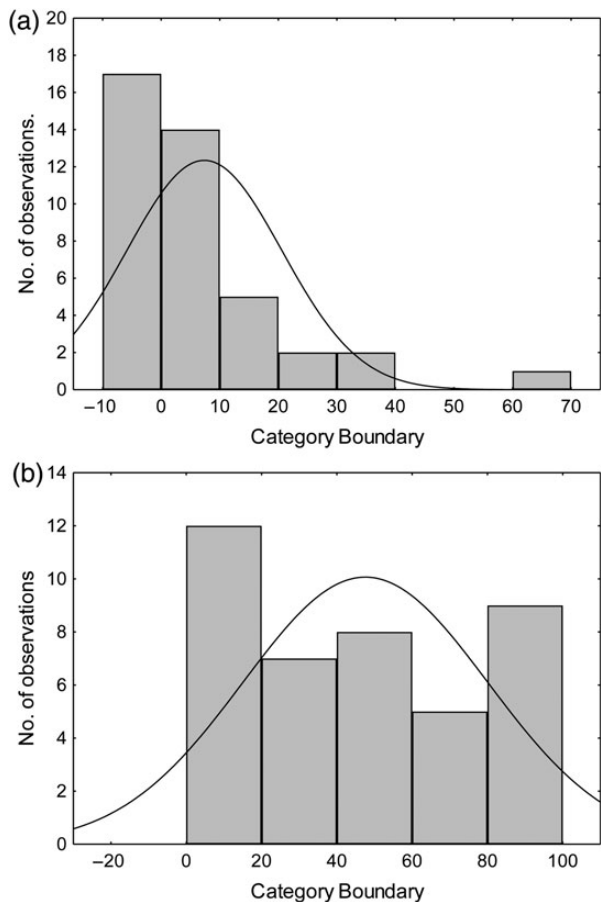


Fig. 3. Frequency distributions of (a) minimum, and (b) maximum percentages of dead zooplankton observed in freshwater environments. Lines are expected normal distributions for reference.

where \mathcal{Y} is the number of carcasses collected in the trap per day ($\text{ind.}\cdot\text{day}^{-1}$), S is the mouth area of the collector (m^2), and y^* is the abundance of carcasses ($\text{ind.}\cdot\text{m}^{-3}$) at trap depth.

This method of mortality estimation is inevitably prone to errors because of the inherently small precision of estimation of zooplankton abundance by field sampling and carcass sinking by sediment traps. However, ways to minimize these errors have been suggested (Dubovskaya, 2008b): (i) time of trap exposure should be ≤ 24 h to increase accuracy and precision of estimation of \mathcal{Y} ; (ii) several traps should be exposed simultaneously as replicates and to increase the total value of S ; (iii) plankton samples at the trap depth should be of a large volume to increase accuracy and precision of y^* ; (iv) the sampling at the trap depth should be done two to four times during the period of trap exposure to increase accuracy and precision of y^* .

This method was used in a reservoir and gave a specific non-predatory mortality rate up to 0.8 day^{-1} for *Daphnia*

(Dubovskaya *et al.*, 2003), considerably higher than senescence-related mortality. This is not unexpected because, as we discuss below, zooplankton can be subject to multiple non-predatory mortality factors *in situ*, which likely hasten their death.

WATER TEMPERATURE

There is evidence of increasing non-predatory mortality within a community caused by increasing water temperature (Elliott and Tang, 2011b). For instance, the abundance of zooplankton carcasses downstream of a warm water discharge from a thermal power station was two to seven times higher than that upstream (Sergeeva *et al.*, 1989). Increase in mortality of 'spring' clones of *Daphnia magna* (*in situ* temperature 4.4°C) was observed in a life-table experiment at 30°C under high food quality and quantity (Giebelhausen and Lampert, 2001). In the Chesapeake Bay, an exceptionally warm summer in 2005 (average water temperature 27.5°C , maximum 33.4°C) coincided with a high percentage of dead copepods (average 32%) (Tang *et al.*, 2006a). Seasonal variations of water temperature may also be important. For example, water temperature in the previous winter, early spring and particularly early summer were found to affect the magnitude of summer predatory and non-predatory mortality of *Daphnia* (Benndorf *et al.*, 2001; Wagner *et al.*, 2004).

WIND AND CURRENTS

Wind affects plankton mortality via waves and currents. For instance, mortality of *Diaphanosoma brachyurum* correlated positively with wind speed (Herzig, 1974; cited by Boersma *et al.*, 1996). On a day of strong wind and waves, peaks of dead *Daphnia* (ca. 20%) and copepodites of *Cyclops* (16%) were observed in the shallow Bugach reservoir (Dubovskaya, 2005). Boersma *et al.* (Boersma *et al.*, 1996) cited reports of large amounts of air-locked *Daphnia* along the foam lines of Langmuir circulations, and patches of millions of doomed *Daphnia* individuals trapped at the surface. Zagarese *et al.* (Zagarese *et al.*, 1998) asserted that in shallow lakes, moderate wind is sufficient to generate turbulence velocity $> 1 \text{ m min}^{-1}$, which is significantly higher than the cruising speed of crustacean zooplankton, $\sim 12\text{--}24 \text{ cm min}^{-1}$, and suspends zooplankton close to the surface, exposing them to potentially damaging solar radiation.

Enhanced mortality of lentic zooplankton has been found in rivers and lake and reservoir outflows. For instance, increasing current velocity in Petrokrepost Bay of Lake Ladoga increased the percentages of dead individuals up to 20% among the cladocerans, up to 40% in

rotifers and up to 50% in copepods (Telesh, 1986; Table III). Only 1% of the cladocerans and 10% of the copepods from the waters of Lake Ladoga and the Neva River reached the Neva Bay alive (Telesh, 1986). During passage through the high-pressure dam of Krasnoyarsk Hydroelectric Power Station in the Yenisei River, the percentage of dead zooplankton increased from 3% in the reservoir to 6% in the river after the dam (Gladyshev *et al.*, 2003b; Dubovskaya *et al.*, 2004). Afterwards, in the fast-flowing Yenisei River (current velocity 1–4 m s⁻¹), ~30 km downstream from the dam, percentages of zooplankton carcasses increased to an average of 11% (Gladyshev *et al.*, 2003b; Dubovskaya *et al.*, 2004). It is estimated that the threshold current velocity for lentic zooplankton was 0.2–0.25 m s⁻¹ (Greze, 1957; Bityukov, 1965; Dubovskaya, 1987, 2009). Above this threshold, lentic zooplankton, which are introduced into the rivers, will die. Besides lake–river interfaces, enhanced zooplankton mortality has also been observed at river fronts in coastal areas (Zelezinskaya, 1966; Koval, 1984; Tang *et al.*, 2006a).

TURBULENCE

The sublethal effects of turbulence on excretion, heart beats (Alcaraz and Saiz, 1991), development (Saiz and Alcaraz, 1991) and growth efficiency (Saiz *et al.*, 1992) have usually been studied in the laboratory by exposing zooplankton to moderate turbulence intensity within the range normally found in coastal zones and tidal fronts (energy dissipation rates = 0.05–0.15 cm² s⁻³, Kjørboe and Saiz, 1995). In comparison, the impacts of intense episodic turbulence such as that caused by storms and boating activities are rarely evaluated. Tóth *et al.* (Tóth *et al.*, 2011) showed that in Lake Balaton, enhanced turbulence due to low water level after a long drought coincided with low zooplankton abundances. A study in the Chesapeake Bay showed that the prevalence of dead copepods was significantly higher (14.3%) within the wakes of passing motorized boats than outside the wakes (7.7%), and it was also higher (34%) along a navigation channel than in the adjacent quiescent waters (5.3–5.9%) (Bickel *et al.*, 2011). Complementary experiments by both research groups confirmed a positive correlation between non-predatory mortality and turbulence intensity (Bickel *et al.*, 2011; Tóth *et al.*, 2011). Recreational and commercial boating activities can be high in lakes and rivers; frequency and intensity of storms are also expected to increase due to climate change. The effects of intense episodic turbulence, both natural and man-made, on zooplankton mortality deserve further investigation.

TOXICITY

Cyanobacterial blooms are expected to increase in lakes and ponds in response to climate change (Paerl and Huisman, 2009), raising concerns that these blooms may be harmful to zooplankton communities. Direct observations of zooplankton mortality due to cyanobacterial toxicity, however, are sparse (Haney and Lampert, 2013), and reports have been ambiguous and contradictory at times (Wilson *et al.*, 2006; Tillmanns *et al.*, 2008). For example, in the Bugach reservoir, no correlation was found between zooplankton non-predatory mortality and cyanobacterial toxicity (Dubovskaya *et al.*, 2002). There is also evidence of adaptation of zooplankton to cyanobacterial toxins, allowing them to avoid or mitigate any toxicity effects (e.g. Hairston *et al.*, 2001; Sarnelle and Wilson, 2005; Wojtal-Frankiewicz *et al.*, 2013). On the other hand, mass death of *Daphnia* was observed in Lake Hallwilersee, probably caused by toxins (oligopeptides) from *Planktothrix rubescens* (Baumann and Jüttner, 2008). Semenova (Semenova, 2011) reported an average of 6.7% dead zooplankton in the Curonian Lagoon in a year with a heavy cyanobacterial bloom, in contrast to only 1.9% in a year without blooms. Other phytoplankton species may also have toxic effects: Naumova (Naumova, 2006; Table III) reported as high as 80% dead nauplii of *Epischura baikalensis* in Lake Baikal in years of high abundance of the diatom *Melosira baikalensis*, and probable deleterious effects of cytotoxic compound of marine diatoms on juvenile copepods have been discussed extensively in the last two decades (Ianora and Miralto, 2010 and references therein). Many of the purportedly toxic phytoplankton species are also considered inferior food for zooplankton, making the distinction between toxic effects and nutritional effects difficult (de Bernardi and Giussani, 1990; Jónasdóttir *et al.*, 1998).

Mortality due to anthropogenic toxins (xenobiotics) is well documented in the laboratory, and is very likely happening in polluted natural water bodies (Hanazato and Dodson, 1995; Ivanova and Telesh, 1996; Relyea, 2009). For instance, Gladyshev (Gladyshev, 1993) found an increased percentage of dead zooplankton, up to 34% (Table III), in the Krasnoyarsk reservoir at a site under the influence of village wastewaters. Similarly, in Lake Galichskoie, the maximum percentage of zooplankton carcasses (15%) occurred at polluted sites, while the minimum (0.17%) was at unpolluted sites (Smelskaya, 1995; Table III).

PARASITISM

Parasitism is widespread among freshwater (Ebert *et al.*, 2001; Bittner *et al.*, 2002) and marine zooplankton

(Skovgaard and Saiz, 2006). In three small ponds in southern England, three *Daphnia* species were infected by 17 species of endoparasites, and the mean percentage of infected adults was up to 84.7% (Stirnadel and Ebert, 1997). A rich and highly prevalent community of parasites in *D. magna* was found in both fishless ponds (Stirnadel and Ebert, 1997) and ponds with fish (Decaestecker et al., 2005), despite the expectation that planktivorous fishes would selectively cull infected *Daphnia* (Duffy et al., 2012). While most parasites affect the hosts by reducing their fecundity and reproduction (e.g. Stirnadel and Ebert, 1997; Decaestecker et al., 2005), cases of fatality have been reported. In microcosms, *D. galeata* from Lake Constance infected by the protist (haplosporidium) *Caullerya mesnili* died in 11–12 weeks, but uninfected ones had a longer life span (Bittner et al., 2002). Outbreaks of fungal infection also caused massive mortality of the cladoceran *Penilia avirostris* in the Black Sea, leading to a high percentage of carcasses (64%; Table II) and a ‘rain of carcasses’ into sediment traps (Zelezinskaya, 1966). Johnson et al. (Johnson et al., 2009) estimated that a chytrid epidemic (*Polycaryum leave*) reduced the population density of *D. pulex* by an average of ca. 10%, and up to 50% during peak infection levels.

Besides endoparasites, zooplankton can be infected by epibionts such as algae, ciliates, fungi and bacteria. Allen et al. (Allen et al., 1993) reported an increased total mortality of *Daphnia* in Lake Mendota due to high infestation by the epibiont diatom *Synedra cyclopum*. Pigmented algal epibionts also make the zooplankton more visible to planktivorous fish and thereby enhance predatory, rather than non-predatory, mortality (Willey et al., 1990, 1993; Dubovskaya et al., 2005). Indeed, in the Bugach reservoir, there was no correlation between the percentage of dead zooplankton and various indices of infestation by epibionts (Dubovskaya et al., 2005).

FOOD QUANTITY AND QUALITY

Limitation by food quantity is an evident and well-known cause of non-predatory mortality (Luecke et al., 1990; Boersma et al., 1996). A well-documented phenomenon in temperate lakes is the mid-summer decline of zooplankton (Threlkeld, 1979 and references therein) that follows the clear water phase when food supply becomes scarce, and recent studies have shown that this decline is caused at least partly by starvation (Hessen, 1989; Hülsmann and Weiler, 2000; Wagner et al., 2004).

Besides food quantity, food quality in terms of the C:N:P ratio, essential polyunsaturated fatty acids (PUFA) and sterols is also a key factor regulating zooplankton populations (e.g. Müller-Navarra, 1995; Wacker and Von

Elert, 2001; Martin-Creuzburg et al., 2005; Gladyshev et al., 2006). It has been suggested that high non-predatory mortality of *Daphnia* in Bautzen Reservoir in the summer was the result of low food quality rather than quantity (Hülsmann, 2001, 2003; Hülsmann and Voigt, 2002). In the Bugach Reservoir, a shortage of the essential PUFA eicosapentaenoic acid (EPA, 20:5:ω3) in seston was the most significant contributor to zooplankton non-predatory mortality among all other environmental factors (Gladyshev et al., 2003c; Dubovskaya, 2008a).

SINKING OF ZOOPLANKTON CARCASSES

Regardless of the cause of death, a zooplankton carcass may continue to influence water column biogeochemistry via decomposition and sinking. The sinking of small particles within a laminar flow regime can be described by Stokes’ law:

$$U_S = \frac{1}{18} \frac{BL^2}{\nu}, \quad (3)$$

where U_S is the terminal velocity, L is the particle size, $B = g\Delta\rho/\rho_w$ is the downward force due to gravity, g , $\Delta\rho = (\rho_p - \rho_w)$ is the ‘excess density’, i.e. the particle density ρ_p minus that of surrounding water ρ_w . For large objects, the Reynolds number $Re = U_S Lv^{-1} \gg 1$ and the flow around the object become unstable (turbulent), in which case the sinking rate can be parameterized as:

$$U_S^2 = C_D^{-1}BL, \quad (4)$$

where C_D is an empirical drag coefficient.

Equation (3) is usually applied for particles with $Re < 0.5$, such as phytoplankton cells and zooplankton fecal pellets, whereas equation (4) is applicable to large sinking bodies with $Re \gg 1$, such as dead fish. Mesozooplankton fall into the uncertainty area of $Re \approx 1$. To approximate this intermediate flow regime, the following formula was derived by Allen (Allen, 1900):

$$B \sim L^{-3/2}\nu^{1/2}U_S^{3/2} \text{ or } U_S = C_S^{*-2/3}B^{2/3}L\nu^{-1/3} \quad (5)$$

Kirillin et al. (Kirillin et al., 2012) proposed an alternative formula yielding similar results:

$$U_S = \frac{BL^2}{C_S\nu + (C_D BL^3)^{1/2}}, \quad (6)$$

with C_S and C_D being empirical constants. Equation (6) corresponds to equation (3) for small L and $C_S = 18$, and to equation (4) for large L ; it therefore provides a smooth

interpolation between the two asymptotic regimes. Brooks and Hutchinson (Brooks and Hutchinson, 1950) analyzed carcass sinking rate data for different *Daphnia* species, and found that equation (3) held true for Re as high as 4. Only for the large individuals with Re varying from 10 to 16, that equation (5) gave better results. Hutchinson (Hutchinson, 1967) analyzed the data for *D. schodleri* (Hantschmann, 1961) and reported a transition to the intermediate regime for individuals ≥ 1.6 mm. Based on empirical data, Kirillin *et al.* (Kirillin *et al.*, 2012) found the difference between equations (3) and (6) to be negligible for $Re = 0.5–1.0$. Thus, the sinking rates roughly obey Stokes' law for all but the largest specimens, with a typical value of 50–150 m day⁻¹ (Fox and Mitchell, 1953; Stepanov and Svetlichnyi, 1981; Kirillin *et al.*, 2012). The hydrodynamic characteristics of zooplankton carcasses can be further modified by the opening and closing of carapaces and antennae: The sinking rate of *Daphnia* with spread antennae decreased by a factor of 0.7 compared with that with closed antennae (Eyden, 1923). Some individuals of *D. cucullata* opened their carapace upon death, creating a 'parachute effect' and reducing the sinking rate by a factor of 0.4 (Kirillin *et al.*, 2012).

Compared with laboratory measurements, *in situ* methods of sinking rate estimation yield much lower values: The average sinking rate of plankton in the epilimnion of a lake was only 1–4 m day⁻¹ (Bloesch and Burns, 1980), and sinking rate of dead copepods in the Black Sea was 4–6 m day⁻¹ (Zelezinskaya, 1966). Umnova (Umnova, 1999), summarizing many *in situ* measurements, concluded that most particles sank at ca. 0.1 m day⁻¹. Zooplankton carcasses caught in shallow plankton net tows also suggest that some carcasses may remain in the upper water column for an indefinite time (Bickel *et al.*, 2009; Elliott and Tang, 2011a). A study in the Japan Sea even found an accumulation of copepod carcasses just below the thermocline, where they may remain for months (Terazaki and Wada, 1988). The major environmental factors decreasing sinking rate are small-scale turbulence, density stratification and microbial degradation. A model of stochastically homogeneous and isotropic turbulent fluctuations based on empirical data produced a slightly shorter average carcass residence time in the upper half of a well-mixed epilimnion, and a longer residence time in the lower part (Kirillin *et al.*, 2012). Thus, the turbulence effect on the mean sinking rate was weak, but the residence time of individual carcasses diverged strongly from the mean value: $\sim 10\%$ of the carcasses stayed in the epilimnion for twice as long as the average residence time, and $\sim 1\%$ stayed four times longer before settling to the hypolimnion. In shallow unstratified lakes without a hypolimnion, turbulence may significantly increase the residence time of zooplankton carcasses in the water column,

which is confirmed by the correlation between sediment trap data and wind velocity in the shallow Bugach reservoir (Dubovskaya *et al.*, 2003).

Stratification mainly influences sinking when the carcasses encounter higher viscosity in the hypolimnion, whereas its effect on the carcass excess density is assumed to be small. The actual effect of stratification on excess density is determined to a high degree by thermal expansion of the carcasses when they reach the cold hypolimnion, which is practically unknown and is usually assumed to be equal to thermal expansion of water, but this is apparently not true (Visser and Jónasdóttir, 1999; Campbell and Dower, 2003).

Elliott *et al.* (Elliott *et al.*, 2010) developed a model of microbial decomposition of carcasses and estimated that sinking copepod carcasses would degrade to zero excess density within the first 300 m. Adopting that model, Kirillin *et al.* (Kirillin *et al.*, 2012) found a remarkable decrease in the termination depth of sinking (depth at which the carcasses achieve neutral buoyancy) with a slight warming of the hypolimnion: An increase in water temperature from 5 to 7°C resulted in a two-fold decrease in the termination depth (from 80 to 40 m for an initial excess density of 25 kg⁻³). This result implies that the climate-driven hypolimnion warming in temperate lakes could lead to a strong increase in water column carbon retention in the form of zooplankton carcasses.

CARCASS FLUX TO THE BENTHOS

Traditionally, zooplankton bodies found in sediment traps are assumed to be swimmers and excluded from gravitational flux calculations (Buesseler *et al.*, 2007). However, zooplankton carcasses are part of the true passive flux and can be important outside the phytoplankton growth periods in coastal and continental shelf areas (Sampei *et al.*, 2009, 2012; Frangoulis *et al.*, 2011). Using scuba diving and sediment trap deployment in Lake Constance, several investigators showed that zooplankton carcasses were important components of sinking aggregates especially during the clear water phase (Grossart and Simon, 1993; Grossart *et al.*, 1997; Gries and Güde, 1999). Gries and Güde (Gries and Güde, 1999) reported the sedimentation of infected and dead *D. galeata* to be as high as 3000 ind. m⁻² day⁻¹ during the time when the pelagic population decreased from 160 000 to 10 000 ind. m⁻². Likewise, in Bugach reservoir, an increase in trap-collected *Daphnia* carcasses was related to an increase in non-predatory mortality of the pelagic population (Dubovskaya *et al.*, 2003). These observations, albeit limited, suggest that sinking zooplankton carcasses can be important

vectors for transporting organic matter to the bottom water, especially in shallow lakes and reservoirs.

In marine systems where mass deposition of zooplankton carcasses has been observed, benthic scavengers were able to exploit the carcasses for food (Zajaczkowski and Legezynska, 2001; Lebrato and Jones, 2009). In temperate lakes, zooplankton often undergo a regular boom-and-bust cycle characterized by a rapid population decline during the clear water phase (Voigt and Hülsmann, 2001; Hülsmann, 2003); one may therefore suggest that seasonal deposition of zooplankton carcasses represents a predictable and important pulse of food to the benthos.

CARCASS-MEDIATED MICROBIAL PROCESSES

Given that zooplankton biomass tends to have a much lower C:N:P ratio than phytoplankton and detritus (Redfield *et al.*, 1966; Elser and Hassett, 1994), it is conceivable that zooplankton carcasses represent a high quality organic substrate source for bacteria. Harding (Harding, 1973) suggested that zooplankton carcasses are decomposed primarily by bacteria colonizing from the outside, rather than bacteria originally carried by the zooplankton. More recently, microbial decomposition of freshwater zooplankton carcasses has been studied in greater detail: as expected, newly deceased zooplankton function as microbial hotspots, supporting elevated bacterial enzymatic activities and production in the water column (Tang *et al.*, 2006b; Bickel and Tang, 2010). The bacterial community composition associated with decomposing carcasses also shifted, indicating that selective bacterial species were more capable of exploiting zooplankton carcasses (Tang *et al.*, 2006b). When bacteria were inhibited by antibiotics, extensive fungal colonization of the carcasses was observed, pointing to a hitherto unknown role of aquatic fungi in turning over zooplankton carcass carbon (Tang *et al.*, 2006b).

In a study that compared microbial decomposition of cladoceran and copepod carcasses in lake water, cladoceran carcasses were initially colonized by bacteria more quickly, suggesting that their carapace was more penetrable by bacteria (Tang *et al.*, 2009). Interestingly, copepod carcass carbon was turned over at a higher rate, suggesting that copepod tissues were more labile. The ambient environment also made a difference: Carcass carbon was turned over more quickly in a eutrophic lake than in an oligotrophic lake (Tang *et al.*, 2009). Hence, while microbial decomposition of carcasses will channel zooplankton carbon to the microbial loop, the strength of this pathway will depend on the zooplankton species, ambient environmental conditions and residence time.

The role of carcasses as hotspots of microbial activity might have an important indirect effect on the aquatic carbon cycle. In aquatic ecosystems, autochthonous recalcitrant organic matter (ROM) might represent up to 80% of the total organic carbon (Guenet *et al.*, 2010). Mineralization of ROM is believed to be accelerated in the presence of labile organic matter (LOM) that supplies energy to decomposers for the production of extracellular enzymes, which in turn degrade ROM into simpler catabolites (Guenet *et al.*, 2010). We might speculate that carcasses of freshly dead zooplankton as a source of LOM might provide such a 'priming effect' for ROM decomposition in the water column.

CONCLUSIONS AND FUTURE DIRECTIONS

The difficulty in separating live and dead zooplankton in field samples may lead researchers to ignore carcasses out of convenience, and the challenge in identifying the causes of non-predatory mortality can be daunting. Nevertheless, as pointed out by the eminent limnologist Robert G. Wetzel (Wetzel, 1995): '*Just because we cannot measure non-predatory mortality well does not mean it does not exist or even dominate at most times of the year.*' There has been a growing interest in studying zooplankton carcasses in marine systems in recent years (e.g. Elliott *et al.*, 2013; Dasse *et al.*, 2014; Martínez *et al.*, 2014), which will add to our knowledge of the global non-predatory mortality among marine zooplankton (Hirst and Kiørboe, 2002). Marine and freshwater zooplankton communities tend to be dominated by taxa with very different life cycle strategies: marine systems are usually dominated by sexually reproducing copepods with longer life cycles and distinct developmental stages, whereas freshwater systems are usually dominated by parthenogenetic cladocerans with relatively high intrinsic growth rates (Allan, 1976). Comparison of the global non-predatory mortality rates and patterns between the two systems and their driving mechanisms will be an important research direction.

Global climate change is already having noticeable effects on freshwater ecosystems such as changes in hydrology, water chemistry, species diversity and phenology (Carpenter *et al.*, 1992; Winder and Schindler, 2004; Heino *et al.*, 2009). Non-predatory zooplankton mortality is expected to increase due to rising water temperature, increasing cyanobacterial blooms and weakened coupling between phytoplankton and zooplankton production cycles. Warmer temperatures may also promote the emergence of new parasites and diseases (Lafferty, 2009) and changes in fish recruitment (Lehtonen, 1996). These changes will likely alter the relative importance of

predatory vs. non-predatory mortality among zooplankton, and the consequent trophic transfer, nutrient and carbon fluxes. Recent advances in live/dead sorting methods and modeling provide researchers with the necessary tools to study this important but under-appreciated topic.

SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

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