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**SHIFTS IN MASS-SCALING OF RESPIRATION, FEEDING, AND GROWTH RATES  
ACROSS LIFE-FORM TRANSITIONS IN MARINE PELAGIC ORGANISMS**

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23 ABSTRACT: The metabolic rate of organisms may either be viewed as a basic property from which  
24 other vital rates and many ecological patterns emerge and that follows a universal allometric mass  
25 scaling law; or it may be considered a property of the organism that emerges as a result of the  
26 adaptation to the environment, with consequently less universal mass scaling properties. Here, we  
27 examine the mass scaling of respiration and maximum feeding (clearance and ingestion rates) and  
28 growth rates of heterotrophic pelagic organisms over a  $\sim 10^{15}$  range in body mass. We show that  
29 clearance and respiration rates have life-form-dependent allometries that have similar scaling but  
30 different intercepts, such that the mass-specific rates converge on a rather narrow size-independent  
31 range. In contrast, ingestion and growth rates follow a near-universal taxa-independent  $\sim 3/4$  mass  
32 scaling power law. We argue that the declining mass-specific clearance rates with size within taxa is  
33 related to the inherent decrease in feeding efficiency of any particular feeding mode. The transitions  
34 between feeding mode and simultaneous transitions in clearance and respiration rates may then  
35 represent adaptations to the food environment and be the result of the optimization of tradeoffs that  
36 allow sufficient feeding and growth rates to balance mortality.

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## Introduction

The vital rates of organisms depend on their size: feeding, metabolism, and growth rates all increase allometrically with organism size, typically such that the mass-specific rates decline with body mass (Peters 1983). This size dependency of energy flow and transformation ultimately determines the size structure of ecosystems (Andersen and Beyer 2006). This has probably been most explicitly described in the Metabolic Theory of Ecology (MTE), which argues that the metabolic rate is the fundamental property of organisms that governs many other patterns in ecology, from growth and feeding rates, life histories, population growth, ecosystem structure and productivity (Brown et al. 2004). The MTE rationalizes Kleiber's  $3/4$  power law for metabolic scaling from first principles, based on ideas of fractal branching distribution networks (e.g. West et al. 1997) and it argues that the law applies universally, from the smallest to the largest organisms (West and Brown 2005).

Empirically and/or theoretically supported scaling laws have similarly been proposed for other vital rates, such as feeding and growth rates, both within and across taxa (e.g., Fenchel 1986; Hansen et al. 1997; Ernest et al. 2003). Theoreticians still argue about the rationale of MTE, particularly the foundations for the metabolic scaling law (reviewed by Glazier 2010), and empiricists have not convincingly been able to decide on the magnitude and generality of the exponent of the power law, nor on the existence of one universal metabolic scaling law (Hemmingsen 1960; Banse 1982; DeLong et al. 2010). In fact, recent evidence suggests that mass-specific metabolic rates vary within a rather narrow range due to transitions in scaling properties between life forms (Makarieva et al. 2008).

Implicit in the MTE is that organism properties and life histories follow from metabolic constraints. However, organism biology, including life histories, feeding and metabolic rates, are not only

determined by internal constraints governed by organism size, but are also the result of adaptations to the environment in which the organism lives. One can argue that the metabolic rate of an organism may at least partly be an emergent rather than a fundamental property. This viewpoint is maintained by competing metabolic theories, e.g. the Dynamic Energy Budget (Kooijman 1986; Kearney and White 2012) and the Metabolic-level Boundaries hypotheses (Glazier 2010), and lead to predictions of different and variable metabolic scaling relations (exponents  $2/3$  to  $1$ ).

The most fundamental activities of any organism, viz. to eat, survive, grow and reproduce, are interrelated through tradeoffs and shaped by natural selection to optimize the fitness of the individual in the environment. The same environment is experienced differently by organisms of different sizes. For pelagic organisms, for example, fundamental properties of the environment depend on the size of the organism. Large organisms live in a world governed by inertia and where mass transport is by advection, while small organisms experience the same environment as viscous and transport of food and solutes is dominated by diffusion processes. The availability of food in the ocean is typically very low compared to terrestrial systems and generally decreases with size of pelagic organisms, and the method and metabolic cost of food collection consequently vary with size (Kjørboe 2011). Furthermore, the optimal allocation of matter and energy to growth, reproduction, maintenance, and defense (survival) may be very different for different life forms and feeding modes, e. g., between gelatinous and non-gelatinous plankton, between unicellular and metazoan zooplankton, or between ambush feeders and cruise feeders. This may lead to different allometries of vital rates between different life forms and organism sizes in the ocean. Similar arguments may apply to organisms living in other environments.



87 Eventually, the rate of food (energy) acquisition may constrain metabolic and other vital rates.  
 88 Feeding rates of pelagic animals vary with food availability and the functional response can be  
 89 characterized by two properties: (i) the maximum clearance rate, which is the imaginary volume of  
 90 water cleared of prey items per unit time when the prey concentration is low; and (ii) the maximum  
 91 ingestion rate, which is the feeding rate at a non-limiting concentration of food. These two  
 92 properties may scale differently with body size: the first is governed by the rate of transport of food  
 93 to the organism, whether dominated by diffusive or advective processes (i.e., feeding current or  
 94 locomotion of the predator); the latter is governed by the rate at which food can be handled and/or  
 95 transported across surfaces. Pelagic organisms are often food limited (Huntley and Boyd 1984;  
 96 Hirst and Bunker 2002; Lopez-Urrutia et al. 2003), and the functional response may be adapted to  
 97 optimize feeding rate in the real ocean. Other vital rates may similarly be adapted to environmental  
 98 conditions with potential consequences for mass scaling properties (e.g. Witting 1995, Pawar et al.  
 99 2012). Examining a variety of rate processes in organisms within a single environment type is a  
 100 clear way to test the degree of universality of scaling.

101  
 102 Here, we test the null hypothesis that different vital rates in pelagic organisms follow similar and  
 103 universal mass-scaling relations, both within and across taxa. We compile data from the published  
 104 literature in order to examine the mass scaling of feeding (maximum clearance and ingestion rates),  
 105 respiration and growth rates of pelagic organisms, from micron sized heterotrophic flagellates, to  
 106 pelagic fish and jellyfish. We show that clearance and respiration rates have taxon- or life-form-  
 107 dependent allometries and that the mass-specific rates converge on a rather narrow size-independent  
 108 range, while maximum ingestion and growth rates are closer to taxon-independent Kleiber-type  
 109 mass scaling.

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## Material and methods

Data on body mass, maximum ingestion and clearance rates, respiration rates and maximum growth rates of animals living in the ocean epipelagic were compiled from the literature, mainly from original papers, but also from previous compilations by other authors. Data were extracted from tables or digitized from graphs. Only measurements made on individuals of known size, or groups of individuals of similar size, were included. Further details on data selection and computation are given below for each of the vital rates. Body sizes were converted to carbon mass using standard conversion factors derived from a taxon-based synthesis (Kjørboe 2013) or other relevant conversions where necessary. We used taxon-specific conversions, thus ignoring differences between species, since these are minute relative to the range of body sizes examined. For example, for 10 pelagic taxa, the coefficient of variation of taxon-specific carbon content averages just 0.3 (Kjørboe 2013), while body masses in our compilation spans about 15 orders of magnitude. Rates were converted to a standard reference temperature of 15°C by assuming a  $Q_{10}$  of 2.8 (Hansen et al. 1997). This is roughly equivalent to assuming an ‘activation energy’,  $E_a$ , of 0.65 eV for the typical temperature interval of the collected data (Acuña et al. 2011). While  $Q_{10}$  and  $E_a$  may both vary between taxa, taxa-specific information is insufficient, and we followed Hansen et al. (1997) and Acuña et al. (2011) in applying a common temperature correction. Altogether we collected 2729 individual estimates of respiration rate, 871 estimates of maximum clearance rate, 327 estimates of maximum ingestion rates, and 852 estimates of maximum growth rates. All data are available in online appendices A-C.

### *Ingestion and clearance rates*

Ingestion and clearance rates depend on both the size and concentration of prey. We preferentially collected measurements taken at several prey concentrations and several types (sizes) of prey,

allowing prey-size specific estimates of maximum ingestion rate (i.e., ingestion rate at an unlimiting prey concentration,  $I_{\max}$ ) and maximum clearance rate (i.e., the clearance rate at a low prey concentration,  $F_{\max}$ ) from fits of functional response models to observations. In many cases we digitized the data from the original papers and fitted an Ivlev model, but when possible we took the model reported. Two functional response models are preferentially used in the literature, Holling type II and Ivlev:

Holling II:

$$I = I_{\max} \frac{F_{\max} C}{I_{\max} + F_{\max} C} \quad (1)$$

Ivlev:

$$I = I_{\max} (1 - \exp(-\frac{F_{\max} C}{I_{\max}})) \quad (2)$$

where  $C$  is the prey concentration, and  $I_{\max}$  and  $F_{\max}$  are the maximum ingestion and clearance rates, respectively. Fits of the two models yield similar parameter estimates and, hence, we did not attempt to refit to a consistently used model. In some cases sigmoid functional response models had originally been fitted to the data; these were of somewhat variable mathematical form but still allowed estimation of the two parameters. This was done mathematically by estimating  $F_{\max}$  as the first derivative of the ingestion formula at the concentration where the second derivative is zero (i.e.  $F_{\max} = dI/dC$  at  $d^2I/dC^2 = 0$ ). In some cases fits of functional response models were not possible due to scarcity of data, but we could often still estimate the maximum clearance and ingestion rates as those reported for low and high prey concentrations respectively.



157 Data allowing prey size specific estimates of  $I_{\max}$  and  $F_{\max}$  were in some cases possible for  
 158 protozoans, copepods, euphausiids, and fish. For these, only data for optimal prey sizes were used  
 159 in the comparative analysis, i.e., the prey size that yielded the highest  $F_{\max}$ . Data for euphausiids  
 160 feeding on phytoplankton were avoided, unless feeding rates on several prey species were available  
 161 and the highest rates could be selected, because feeding rates on zooplankton for most species is  
 162 much higher. Tunicate data were rarely available for several prey concentrations or prey sizes, and  
 163 hence, estimates of  $I_{\max}$  and  $F_{\max}$  for these groups are conservative. The same applies partly to fish  
 164 and jellyfish. Here we used the data compilation of Acuña et al. (2011) as a starting point. For fish  
 165 we selected maximum clearance rates measured at low prey concentration, and consulted the  
 166 original papers to get maximum ingestion rates at high prey concentrations; for jellyfish we did not  
 167 attempt to estimate maximum ingestion rates since feeding rates in jellyfish often do not saturate in  
 168 (short-term) laboratory experiments (e.g. Hanson and Kiørboe 2006). Data for protists were taken  
 169 from Hansen et al. (1997) and supplemented with many new data from the primary literature. Data  
 170 from all other groups were from original papers.

### 172 *Respiration rates*

173 The respiration rate of an organism depends on its feeding and activity levels. For unicellular  
 174 organisms the respiration rate varies mainly with feeding level (e.g. Fenchel 1989), for larger  
 175 organism more so with activity (e.g. Beamish 1978), and in both cases the variation is within about  
 176 one order of magnitude (except for ‘dormant’ stages that in some taxa may reduce their metabolism  
 177 to very low values). Ideally, one would like to compare ‘standard metabolic rates’ (metabolism of  
 178 non-feeding organisms at rest) but in general it has been impossible to account for these factors in a  
 179 standardized and meaningful way. This is because microbes are adapted to a feast and famine  
 180 existence and may go into dormancy when starved. Furthermore, it is often impossible to control for



181 activity in aquatic organisms (many have to move to stay afloat), and often organisms keep  
 182 swimming or generating a feeding current even when starved. Thus, we have rather selected  
 183 ‘routine rates’ (rates recorded when organisms have normal activity), and have avoided  
 184 measurements taken on dormant stages or individuals starved for prolonged periods of time. In all  
 185 cases metabolism has been quantified as rates of oxygen uptake. Data for fish and jellyfish  
 186 respiration were taken from the compilation of Acuña et al. (2011) and the data for protozoans from  
 187 Fenchel and Finlay (1983). Protozoans included ‘free-living’ forms from both fresh and marine  
 188 environments because it was impossible to decide on the habitat of many species. All other data  
 189 were compiled from original papers.

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### *Growth rates*

192 Growth is a function of ingestion and food concentration, as well as ontogeny. In order to  
 193 standardize these rates we only considered food-saturated growth rates of juvenile individuals. For  
 194 protists, we added many new observations to the data compilation of Hansen et al. (1997). For  
 195 metazoans we began with the synthesis of Hirst et al. (2003), screening the compiled data for food  
 196 saturated rates, and adding data from new sources. For fish we compiled data from the primary  
 197 literature. Geometric mean masses were determined for the period in which growth in mass was  
 198 measured, and all rates converted to mass-specific rates.

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## Results

201

### *Respiration rates*

202 The respiration rate of all taxa increases with body mass and, when plotted together, scale  
 203 approximately with body mass (figure. 1A). We also plotted of mass-specific respiration rates since  
 204 these plots better show differences in magnitude and scaling between taxa (figures 1B-E, Online

205 appendix D): the mass-scaling of specific respiration rates within taxa are all consistent with a  
 206 Kleiber-type scaling, i.e., they are near proportional to body mass (carbon) raised to a power around  
 207  $-1/4$  (Table 1). However, the different taxa separate clearly, with subsequently larger taxa having  
 208 increasing lead coefficients (intercepts), such that, overall, specific respiration rates vary within ca.  
 209 2 orders of magnitude around a common value rather than declining with body mass. The  
 210 protozoans have the lowest intercept, the two groups of copepods intermediate values, and other  
 211 crustaceans (euphausiids and amphipods), tunicates, jellyfish and fish, cluster around yet higher  
 212 values. For comparison, we have shown also Kleiber's (1975) relation for terrestrial mammals that  
 213 provide a conservative estimate for marine mammals (e.g. Lavigne et al. 1985); this relation fits into  
 214 the general pattern, and has the highest lead coefficient. The variation in the intercept of the mass  
 215 specific respiration rates vary between protozoans and mammals by more than 3 orders of  
 216 magnitude, inconsistent with a universal scaling law for metabolic rates (i.e., does not adhere to a  
 217 single unified relation that fits both across and within taxa).

218

#### 219 *Clearance and ingestion rates*

220 The variation in maximum clearance rates resembles that of respiration rates: the overall pattern  
 221 suggests that clearance rates scale with body mass; within taxa, mass-specific clearance rates  
 222 decline with body mass (figure 2). Although these power terms are more variable than those for  
 223 metabolic rates, for mass-specific rates they again center around  $-1/4$  (Table 1). Over a 13 order of  
 224 magnitude variation in body mass, average specific clearance rates vary by 3 orders of magnitude.

225

226 The mass-dependency of ingestion rates differs from those of respiration and clearance rates since  
 227 the various taxa converge more closely on a common relationship, with ingestion rate increasing  
 228 approximately with body mass to a power slightly larger than  $3/4$ . Plots of mass-specific ingestion

rates reveal a rather consistent decline across taxa, and the average of power exponents is not significantly different from  $-1/4$  (figure 3, Table 1).

### *Growth rates*

Growth rates, like ingestion rates, converge on a common relation, with growth rate scaling with body mass to a power of about  $3/4$ , or slightly higher. The specific rates show no consistent pattern between taxa and scale with mass with an average power of near  $-1/4$  (figure 4, Online appendix D).

### Discussion

A clear pattern emerges from the rather noisy data: respiration and clearance rates follow taxon-dependent mass-scaling relations that are consistent with a  $3/4$  scaling law. However, when considered across taxa scaling is close to 1. Consequently, the mass-specific respiration rates converge on a rather narrow, size-independent range, with the average rates varying within  $\sim 2$  orders of magnitude over an 18 order of magnitude variation in body mass. A universal  $3/4$  or  $2/3$  scaling law would imply a variation in mass-specific rates by a factor 30,000 to 1,000,000, rather than the ca. 100-fold variation observed. Clearance rates follow a similar pattern, with no systematic size-dependency when compared across taxa, albeit with larger variation between taxa. The Euphausiids (krill-like organisms) appear low; container effects that suppress feeding are known to occur in highly active Euphausiids, and ignoring those the variation in mass specific clearance rates are again just 2 orders of magnitude. Ingestion and growth rates, in contrast, appear to follow more closely a universal  $3/4$  scaling law, with less consistent differences between taxa. These scaling patterns are apparent only when considered over a large range of body sizes. There may be significant deviations in mass scaling, both during ontogeny within a species and between



species (e.g. Glazier 2005, 2006), but such variation is hidden in the present larger scale analysis, which only emphasizes patterns that transcend the smaller-scale variations.

The lack of universality in the intercepts (elevation) of scaling relationships for organism metabolism is not a new observation, but it has been underappreciated for many years (Brown et al. 2004). Hemmingsen (1960) showed that unicellular eukaryotes, exothermic and endothermic organisms follow similar power laws, but have non-overlapping allometries, with endotherms having 2 orders of magnitude higher metabolic rates than unicellular organisms when corrected for body size. Banse (1982) also observed several transitions in metabolic scaling between groups of (mainly) pelagic organism. More recent reports have similarly demonstrated shifts in metabolic scaling between prokaryotes, protists, and metazoans (DeLong et al. 2010). Hemmingsen's groups correspond to the main ones in our material (figure 1) and correspond, respectively, to the 'invention' of multi-cellularity and homeothermy that may change the metabolic requirements of the organism. Our data, however, demonstrate additional and more continuous transitions among the metazoans organisms that may be related to life forms and feeding modes (see below) resulting in a striking similarity in mass-specific respiration rates across the entire range of organisms examined. A similar result was reported by Makarieva et al. (2008) based on an analysis of an extensive respiration data set covering a huge range of organism sizes, life forms and habitats, from the smallest prokaryotes and plants to the largest mammals, and from aquatic to terrestrial environments. The redesigns that produce small shifts in respiration scaling powers, but marked alteration in intercept, are therefore not simply dependent upon the macro-divisions of major evolutionary life history events noted by Hemmingsen (1960) and DeLong et al (2010). They are also attributable to rather more subtle redesigns related to life-form and possibly behavioral transitions. Makarieva et al (2008) argued for the existence of a 'metabolic optimum', a universal



276 metabolic rate magnitude that optimizes the fitness of organisms, but they did not rationalize its  
 277 existence and magnitude.

278

279 Clearance rates show a mass-scaling pattern that resembles that of the respiration rate, i.e., with  $\sim 3/4$   
 280 power relations within taxa, but with size-independent specific clearance rates when all taxa and  
 281 sizes are considered together. This is different from most previous reports, in which clearance rates  
 282 of pelagic organisms were found to scale with mass to a power less than one (e.g., Fenchel 1986;  
 283 Hansen et al. 1997; Saiz and Calbet 2007; Acuna et al. 2011). However, these papers all considered  
 284 a much smaller range of organism sizes and taxa, and hence may be dominated by within-taxa  
 285 patterns. Is it possible to rationalize the taxa-transcending mass scaling of clearance rates? And is it  
 286 possible to define and rationalize a 'clearance optimum', similar to the metabolic optimum? That is,  
 287 a clearance rate magnitude that optimizes the trade-offs associated with feeding: energy gain vs.  
 288 cost in terms of energy and predation risks. The similarity in mass scaling of respiration and  
 289 clearance may suggest a causal relationship, which is what we next want to turn to in this paper.

290

291 One may argue that the clearance or search rate of an organism represents its own effort to acquire  
 292 food. This effort implies energy demanding work as well as energy to produce and maintain food  
 293 collection apparatus and sensory system. Maintenance and food collection may both potentially  
 294 make a significant contribution to the metabolic rate of an organism, and can apply even when that  
 295 effort does not lead to resource acquisition; the machinery has to be maintained, and the organism  
 296 may keep processing water in search for food even in its absence. There are a limited number of  
 297 basic mechanisms used by pelagic organisms to concentrate food from a dilute environment. The  
 298 efficiencies of these mechanisms, in terms of volumes cleared for prey, are inherently different, and  
 299 each becomes less efficient with increasing body size (Kjørboe 2011), potentially explaining the

300 consistent within-taxa decline in mass-specific clearance rates. Larger taxa must switch to more  
 301 efficient and, presumably, more energy demanding feeding modes and prey sensing mechanism to  
 302 compensate for this general decline in efficiency. Food collection mechanisms in small aquatic  
 303 organisms are dominated by ‘cheap’ passive, diffusion-type processes that do not require perception  
 304 of individual prey. As size increases, taxa use more efficient, but expensive active ‘advective’  
 305 processes, such as cruising or generating a feeding current, as well as costly remote prey sensing  
 306 mechanisms (chemical, hydromechanical, and vision). Thus, some small flagellates feeding on  
 307 bacteria may depend mainly on the motility of the bacteria for prey encounter. Flagellates with a  
 308 feeding current may increase prey encounter rate and swimming may enhance food acquisition by  
 309 bringing the flagellate to food patches, but generating a feeding current and swimming at low  
 310 Reynolds numbers is considered energetically inexpensive (Berg 1993; Guasto et al. 2012). The  
 311 larger ciliates use multiple cilia to generate a more efficient feeding current (Magar and Pedley  
 312 2005; Short et al. 2006), which is presumably also more energetically expensive. Moving to the  
 313 multicellular organisms, the small, non-calanoid copepods are mainly ambush feeders, i.e., they  
 314 hang motionless in the water waiting for prey to pass within their perceptive sphere (Kjørboe et al.  
 315 2010). The larger calanoid copepods and euphausiids produce more efficient and energetically  
 316 expensive feeding currents (Kjørboe and Jiang 2013). In contrast to the unicellular flagellates and  
 317 ciliates, the crustaceans (copepods and euphausiids) typically perceive individual prey using chemo-  
 318 or mechanosensors (e.g. Tiselius et al. 2013; Abrahamsen et al. 2010), which requires maintenance  
 319 of relatively advanced and energetically costly sensory systems (Niven and Laughlin 2008). As we  
 320 move further up in size, the ‘inflated’ (high water content) gelatinous plankton have increased  
 321 capture surface areas per unit of organic matter, which allow for high clearance rates (Acuna 2001;  
 322 Acuña et al. 2011), but this is also costly to maintain (Kjørboe 2013). The use of vision by fish  
 323 results in more efficient remote perception of prey and consequently high clearance rates (Kjørboe



2011). While it is not possible to exactly quantify the metabolic expenses associated with the different feeding modes, we know that ‘active’ is more expensive than ‘passive’, and that the processing of sensory information, particularly vision, is metabolically expensive (Laughline et al. 1998). It is striking that the transitions in feeding modes largely follow the transitions in clearance and respiration scaling (figures 1, 2). In fact, the lead coefficients of taxon-specific allometric fits of mass-dependent respiration and clearance are significantly and linearly related (figure 5).

The trade-offs associated with food collection are not limited to the energetic gains and costs of feeding, but there are also associated predation risks (Visser 2007). Any definition of a clearance optimum should consider all tradeoffs together. Kiørboe and Jiang (2013) evaluated these for intermediate-sized zooplankters and found that optimal foraging considerations predict an optimum magnitude and mass-scaling of clearance rates consistent with that observed here, but their analysis was restricted to a limited size range ( $\sim 6$  orders of magnitude) and did not consider size-dependent variation in the availability of food. The average availability of food in the ocean tends to decline with increasing size of the predator (Kiørboe 2011) and, hence, a constant feeding effort (mass-specific clearance rate) implies a decreasing mass-specific ingestion rate with size, as observed. This may be sufficient to maintain a population in the face of mortality, because mortality rates are also declining with organism size in the ocean (Peterson and Wroblewski 1984; McGurk 1986). In fact, specific ingestion rates and growth rates (figures 3,4), as well as intrinsic population growth (Fenchel 1973, Savage et al. 2004) and mortality rates (Peterson and Wroblewski 1984; McGurk 1986) all appear to decline with body mass in a similar manner. Thus, observed differences and similarities in the mass scaling of different vital rates of pelagic organisms appear to be internally consistent. We hypothesize that the clearance rate magnitude and consequent feeding and growth rate is that required to balance mortality in the ocean, and in that sense defines a clearance and

metabolic rate optimum that maximizes the fitness of the organisms. Whatever the causal relation between feeding and metabolism in pelagic organisms, the lack of universal scaling relations has important implications for our understanding and descriptions of pelagic ecosystems.

Our observations and arguments have focused on pelagic organisms, but the mass-scaling of respiration rate found here for pelagic organism appear to mirror that found also for terrestrial organisms (Makarieva et al. 2008). Similar arguments as those applied here may be generalized to cover other environments and transitions in life-forms. For example, adaptations to habitat dimensionality and transitions from sedentary, to surface motility, to flying life styles are all related to both feeding modes and metabolic expenses (e.g. Pawar et al. 2012) and may show similar co-variation in scaling of metabolism and clearance rates. The organisms included in our synthesis have trophic encounters which predominantly occur in 3-dimensions. Pawar et al.'s (2012) mechanistic model of 3D encounters suggests that both consumption rates and search rates (akin to clearance rate) should scale with body mass with a power  $\sim 1$ , but at less than 1 when encounters are in 2D, e.g., for many terrestrial and benthic encounters. There are three important points which challenge Pawar et al.'s (2012) predictions. Firstly, as we observed, maximum clearance rates (search rates) of individual taxa often scale at less than 1 (Figure 2, Table 1), and our observations only matches Pawar et al.'s conclusion when considered across life forms, as in their own data compilation. Secondly, ingestion rates scale with mass both within and across taxa at less than 1 (Figure 3, Table 1). Further support of sub-isometric scaling is found within taxa when re-assessing Pawar et al.'s consumption data for copepods, insects and fish. Together these include the vast majority of their empirical data set, and each of these taxa show scaling of less than 1. The next generation of mechanistic models needs to be developed so as to explain the differences in scaling of feeding and physiological rates which occur at different levels of organization. Indeed, multiple



mechanisms may need to be evoked across organizational hierarchies. In pelagic invertebrates for example, respiration commonly scales near isometrically intra-specifically (Glazier 2005, 2006), but close to  $3/4$  when considered within individual taxa, and more steeply again when considered across multiple taxa (Figure 1, Table 1) (Makarieva et al. 2008). Many models, including Pawar et al. (2012) and the Metabolic Theory of Ecology (Brown et al. 2004) do not make distinctions at these hierarchies, and hence fail to match the patterns observed in nature.

The declining efficiency of each feeding mode with size implies that there is a maximum size above which it becomes impossible for that feeding mode to maintain a sufficient feeding rate. And there must also be a maximum size range for particular life forms or feeding modes. If we consider the 2 order of magnitude variation in specific metabolism and clearance the optimum range and a  $3/4$  mass scaling, then the maximum possible body mass variation within a particular life form is 8 orders of magnitude. This, in fact, corresponds roughly to the size range of each of the following: protozoans, pelagic crustaceans, gelatinous plankton, fish, and mammals.

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Table 1. Size dependency of mass-specific vital rates for pelagic animals.

Group	Specific Respiration rate (ml O <sub>2</sub> mg C <sup>-1</sup> h <sup>-1</sup> )			Specific Clearance rate (ml mg C <sup>-1</sup> h <sup>-1</sup> )			Specific Ingestion rate (µg C mg C <sup>-1</sup> h <sup>-1</sup> )			Specific Growth rate (mg C mg C <sup>-1</sup> h <sup>-1</sup> )		
	Log <i>a</i>	<i>b</i>	<i>n</i>	Log <i>a</i>	<i>b</i>	<i>n</i>	Log <i>a</i>	<i>b</i>	<i>n</i>	Log <i>a</i>	<i>b</i>	<i>n</i>
Protozoa	-0.20 ± 0.37	-0.22 ± 0.07*	129							-2.32 ± 0.30	-0.15 ± 0.05*	76
Flagellates	2.24 ± 2.26	0.17 ± 0.34	22	1.02 ± 1.21	-0.23 ± 0.17*	38	-0.19 ± 0.80	-0.33 ± 0.11*	33	-3.23 ± 0.40	-0.27 ± 0.06*	41
Ciliates	-0.49 ± 0.76	-0.30 ± 0.15*	76	-0.52 ± 1.11	-0.69 ± 0.2*	25	1.29 ± 1.55	-0.16 ± 0.28	14	-1.69 ± 0.65	-0.05 ± 0.12	35
Calanoid copepods	0.54 ± 0.06	-0.22 ± 0.04*	148	2.11 ± 0.31	-0.16 ± 0.12*	52	1.11 ± 0.17	-0.20 ± 0.07*	59	-2.17 ± 0.16	-0.06 ± 0.06*	136
Non-Calanoïd copepods	-0.50 ± 0.34	-0.37 ± 0.09*	26	2.68 ± 1.57	0.10 ± 0.43	26	1.99 ± 1.05	0.19 ± 0.29	23	-3.47 ± 1.67	-0.27 ± 0.41	11
Other crustaceans												
Euphausiids	0.97 ± 0.05	-0.29 ± 0.08*	119	1.71 ± 0.29	-0.37 ± 0.23*	27	1.11 ± 0.56	-0.14 ± 0.58	10			
Amphipods	0.92 ± 0.05	-0.24 ± 0.06*	61									
Chaetognaths				0.96 ± 0.36	-0.69 ± 0.37*	4	-0.06 ± 0.07	-0.56 ± 0.07*	79	-3.19 ± 0.49	-0.35 ± 0.29*	28
Cnidaria + Ctenophores	0.83 ± 0.03	-0.22 ± 0.02*	568	2.68 ± 0.07	-0.11 ± 0.05*	364				-2.41 ± 0.08	-0.15 ± 0.04*	82
Cnidaria	0.86 ± 0.03	-0.21 ± 0.03*	465	2.73 ± 0.07	-0.12 ± 0.05*	342				-2.41 ± 0.14	-0.15 ± 0.10*	31
Ctenophores	0.76 ± 0.05	-0.40 ± 0.06*	100	2.09 ± 0.08	-0.62 ± 0.09*	20				-2.41 ± 0.10	-0.15 ± 0.04*	51
Tunicates	1.00 ± 0.04	-0.11 ± 0.04*	277	2.74 ± 0.08	0.09 ± 0.04*	261	1.91 ± 0.43	0.28 ± 0.20*	72	-3.23 ± 0.44	-0.48 ± 0.19*	46
Pisces	0.96 ± 0.03	-0.22 ± 0.01*	1374	3.24 ± 0.21	-0.24 ± 0.08*	74	0.40 ± 1.09	-0.51 ± 0.32*	45	-2.48 ± 0.04	-0.17 ± 0.02*	331
<b>Average ± 95 % CL</b>		<b>-0.22 ± 0.13</b>			<b>-0.30 ± 0.21</b>			<b>-0.18 ± 0.25</b>			<b>-0.23 ± 0.10</b>	

Regression parameters (± 95 % Confidence limits) for mass-specific vital rate (respiration, clearance, ingestion, growth): log VR = log *a* +

*b* Log M, where VR is the mass specific vital rate, M is the body mass (mg carbon), and *a* and *b* the regression parameters. *n* is the number

of observations, and R<sup>2</sup> is the coefficient of determination. Estimates of *b* that are significantly different from zero have been marked\*. The





averages  $\pm 95\%$  Confidence limits (95 % CL) in the bottom row are of the slopes of individual groups; only the lowest taxonomic units were included in the averaging (e.g., flagellates and ciliates, not protozoans).





## Figure Legends

**Figure 1;** Respiration rates (A) or mass-specific respiration rates (B-E) of various groups of marine pelagic organisms as a function of their body carbon. All rates are converted to a common temperature of 15°C. Panel B compares the regressions with 95% confidence limits for all taxa analyzed, and includes also the line for mammals (Kleiber 1975), while panels (C-E) show the same but with data-points included. The black lines in (A) and (B) are regressions through all data assuming proportionality between respiration rate and body mass or body mass raised to a power of 0.75 (A); or between mass-specific respiration rate and body mass raised to power 0 or -0.25 (B).

**Figure 2:** Maximum clearance rates (A) or mass-specific maximum clearance rates (B-E) of various groups of marine pelagic organisms as a function of their body carbon. All rates are converted to a common temperature of 15°C. Panel (B) compares the regressions of specific rates with 95% confidence limits for all taxa analyzed, while panels (C-E) show the same but with data-points included. The black lines in (A) and (B) are regressions through all data assuming proportionality between maximum clearance rate and body mass or body mass raised to a power of 0.75 (A); or between mass-specific maximum clearance rate and body mass raised to power 0 or -0.25 (B). Panels (C-D)

**Figure 3:** Maximum ingestion rates (A) or mass-specific maximum ingestion rates (B) of various groups of marine pelagic organisms as a function of their body carbon. All rates are converted to a common temperature of 15°C. Panel (B) compares the regressions of specific rates with 95 % confidence limits for the taxa analyzed, and panel (C) the same but with data points included. The black lines in (A) and (B) are regressions through all data assuming proportionality between maximum ingestion rate and body mass or body mass raised to a power of 0.75 (A); or between mass-specific maximum ingestion rate and body mass raised to power 0 or -0.25 (B).

**Figure 4:** Maximum growth rates (A) or mass-specific maximum growth rates (B) of various groups of marine pelagic organisms as a function of their body carbon. All rates are converted to a common temperature of 15°C. Panel B compares the regressions of specific rates with 95 % confidence limits for the taxa analyzed, and panel (C) the same but with data points included. The black lines in (A) and (B) are regressions through all data assuming proportionality between maximum growth rate and body mass or body mass raised to a power of 0.75 (A); or between mass-specific maximum growth rate and body mass raised to power 0 or -0.25 (B).

**Figure 5:** Intercepts values ( $a \pm$  Standard deviation) for allometric regressions of mass-specific clearance rates and mass-specific respiration rates plotted against one another. The allometric regressions assume a Kleiber-type mass scaling (i.e., mass-specific respiration or clearance scale with mass raised to power of -0.25) and are of the form:  $\text{Log}_{10}(VR) = a - 0.25 \text{ Log}_{10}M$ , where  $VR$  is the mass-specific respiration or clearance rate, and  $M$  the body mass (carbon). The regression lines are estimated with equal weight to all observations, or observations weighted with the inverse of variance of the  $a$ -estimate. The regression are:  $Y = 0.93X + 1.56$  (equal weight;  $R^2 = 0.53$ ) and  $Y = 0.88X + 1.48$ . The correlations are in both cases statistically significant with  $p < 0.02$ .

**Online appendices** (These appendices will be deposited in a public data repository):

Online appendix A: Respiration rates of pelagic organisms

Online appendix B: Feeding rates of pelagic organisms

Online appendix C: Growth rates of pelagic organisms





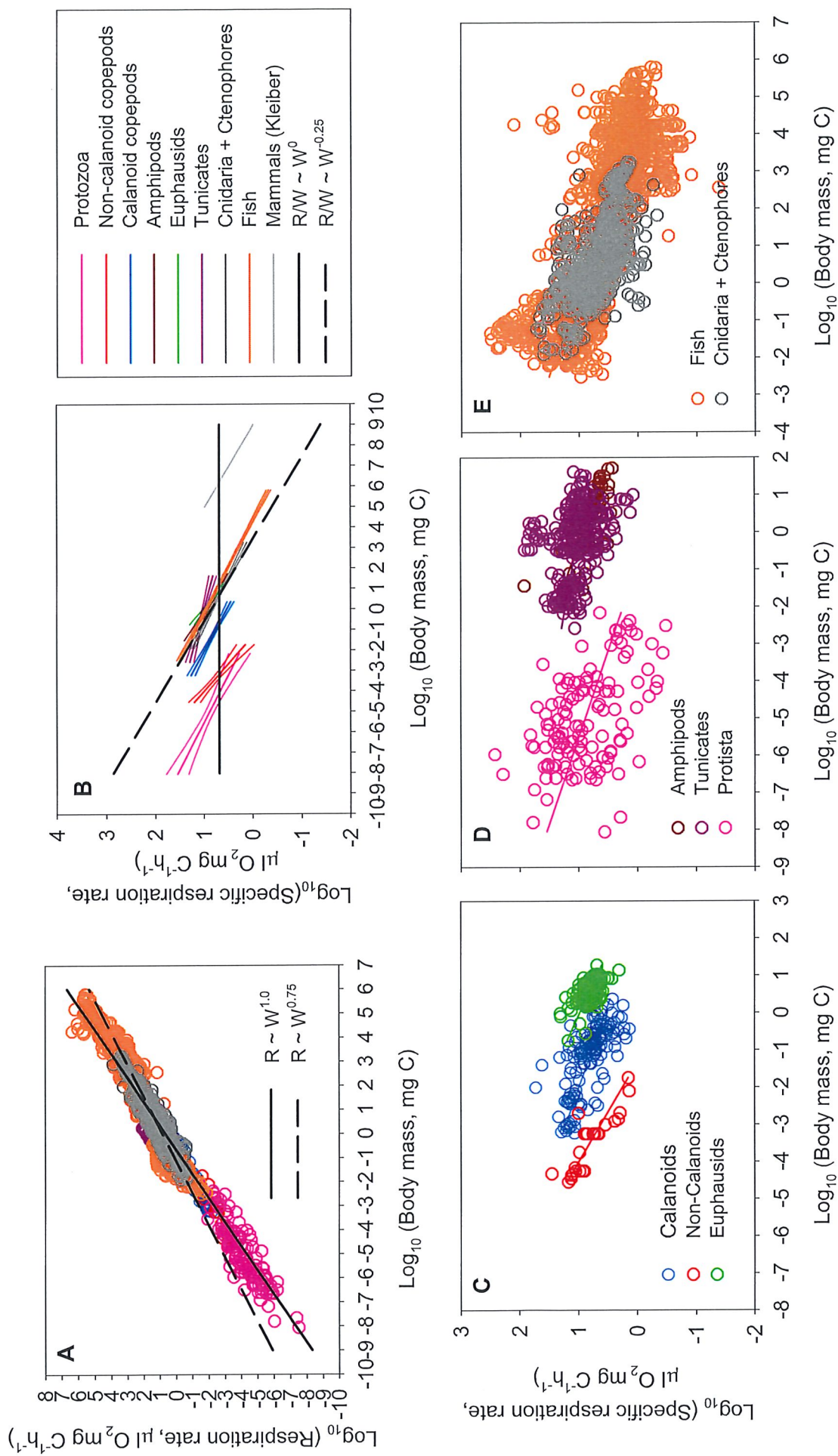
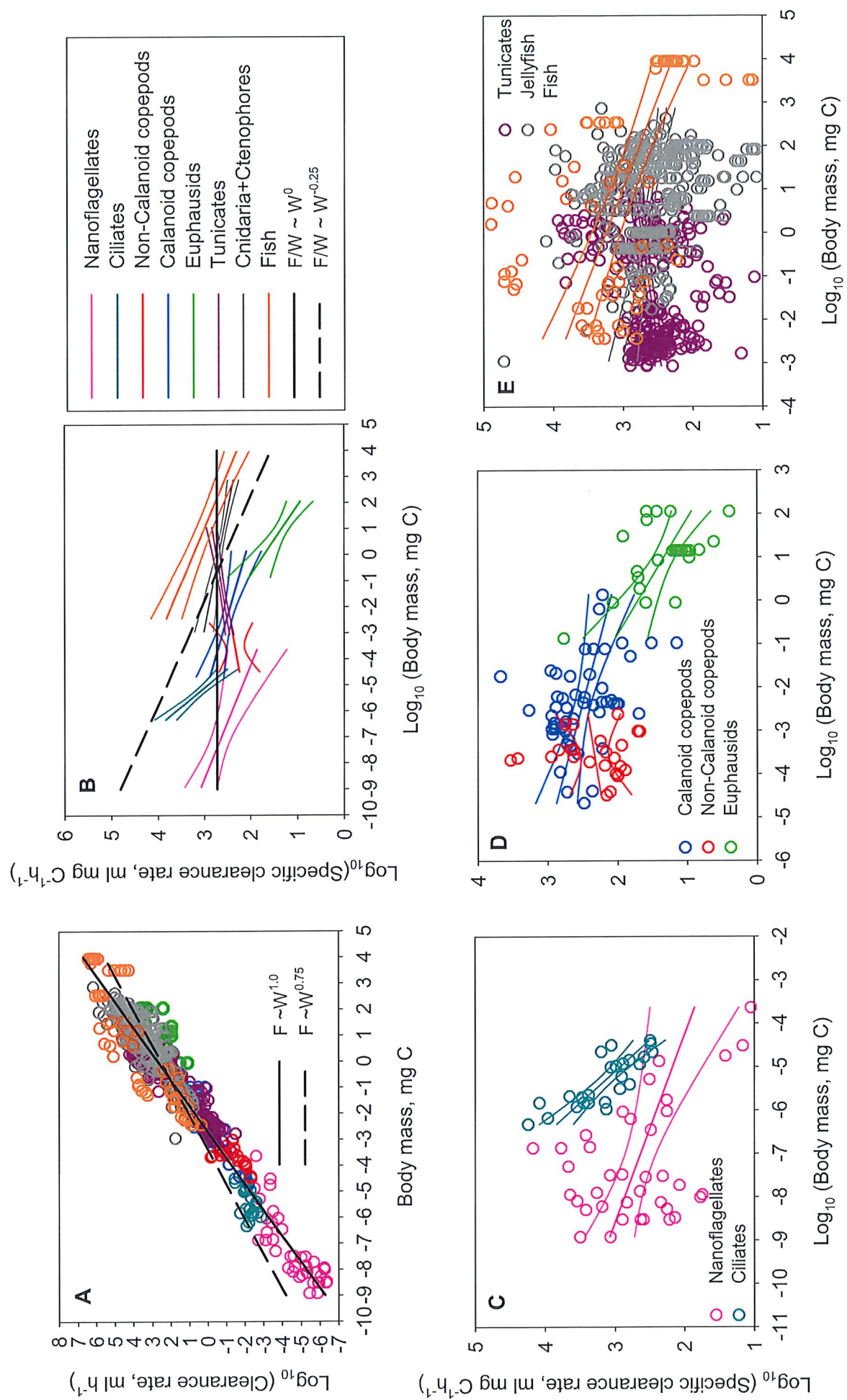


FIG 1





FIG2





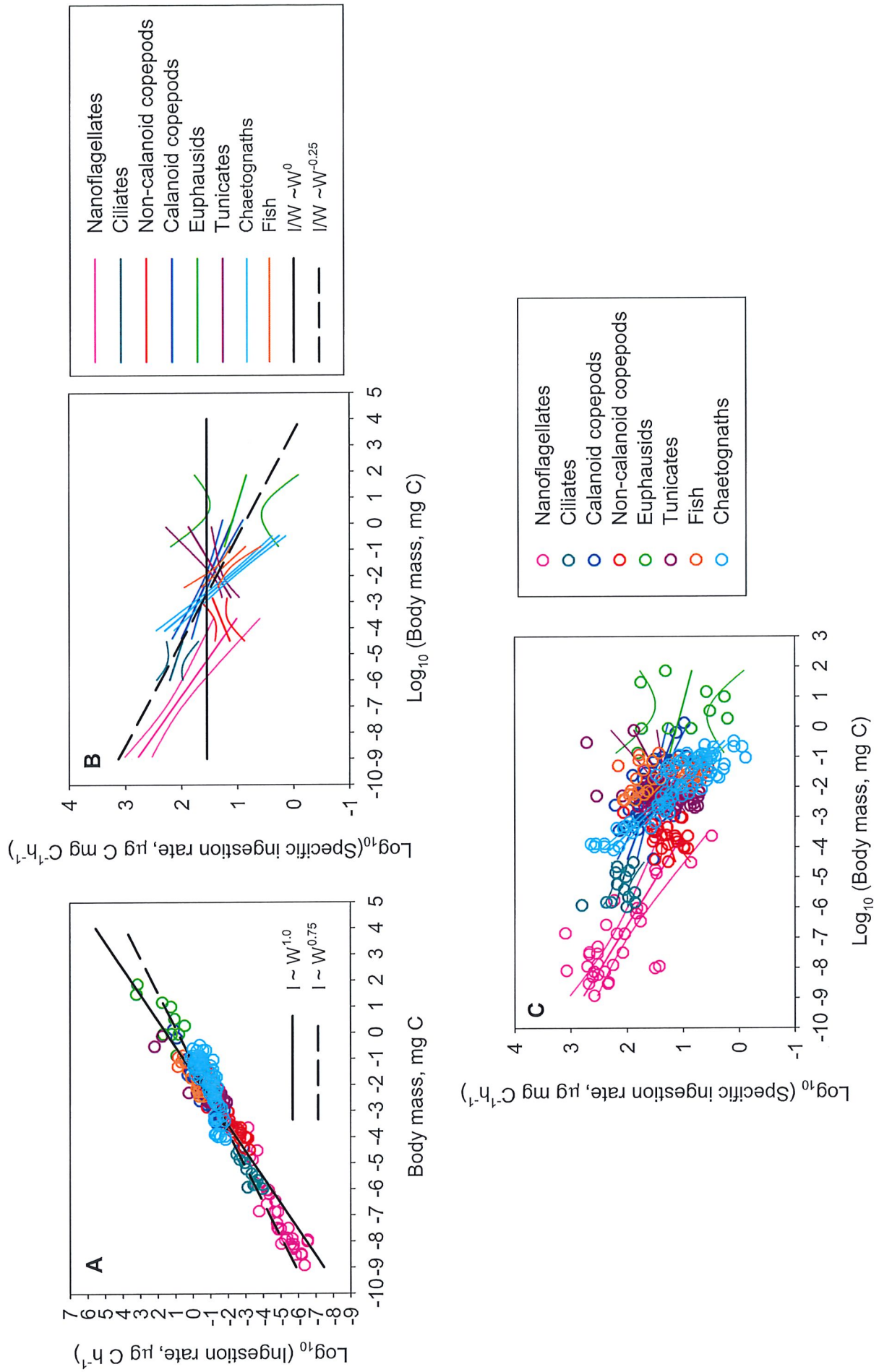


FIG 3





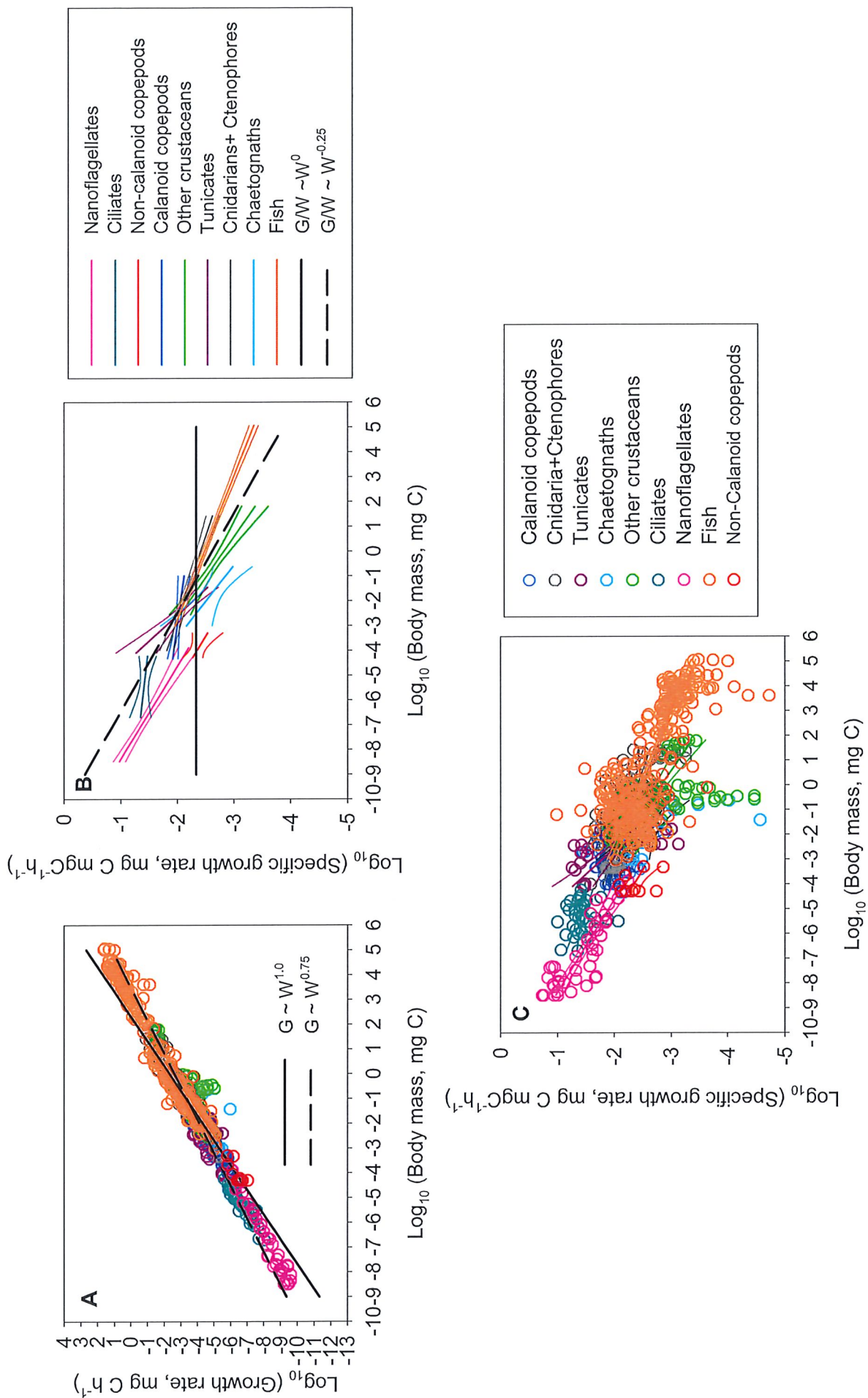


FIG 4





