Characteristic sizes of life in the oceans - from bacteria to whales

Andersen, Ken Haste; Berge, T.; Goncalves, R.; Hartvig, Martin; Heuschele, Jan; Hylander, Samuel; Jacobsen, Nis Sand; Lindemann, Christian; Martens, Erik Andreas; Neuheimer, Anna

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K.H. Andersen, T. Berge, R. J. Gonçalves, M. Hartvig, J. Heuschele, S. Hylander, N.S. Jacobsen, C. Lindemann, E.A. Martens, A.B. Neuheimer, K. Olsson, A. Palacz, F. Prowe, J. Sainmont, S.J. Traving, A.W. Visser, N. Wadhwa, and T. Kiørboe

K.H. Andersen[1,2]: kha@aqua.dtu.dk. Corresponding author, tel. +45 35 88 33 99.

T. Berge[1,8]: tberge@bio.ku.dk

R. J. Gonçalves[1,2,10]: rgon@aqua.dtu.dk

M. Hartvig[2,3,4]: mh@hvig.dk

J. Heuschele[1,2]: janheuschele@gmail.com

S. Hylander[2,9]: samuel.hylander@lnu.se

N.S. Jacobsen[1,2]: nsja@aqua.dtu.dk

C. Lindemann[1,2]: chrli@aqua.dtu.dk

E.A. Martens[1,2,7]: erik.martens@ds.mpg.de

A.B. Neuheimer[2,3,6]: annabn@hawaii.edu

K. Olsson[1,2]: karol@aqua.dtu.dk

A. Palacz[1,2]: arpa@aqua.dtu.dk

F. Prowe[1,2,11]: fprowe@geomar.de

J. Sainmont[1,2]: jusa@aqua.dtu.dk

S.J. Traving[1,8]: sjtraving@bio.ku.dk

A.W. Visser[1,2]: awv@aqua.dtu.dk

N. Wadhwa[1,5]: nawa@fysik.dtu.dk

T. Kiørboe[1,2]: tk@aqua.dtu.dk

1: VKR Centre for Ocean Life.

2: National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Slot, Jægersborg Allé, DK-2920 Charlottenlund, Denmark

3: Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark

4: Systemic Conservation Biology, J.F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Berliner Strasse 28, 37073 Göttingen, Germany

5: Department of Physics, Technical University of Denmark

6: Department of Oceanography, University of Hawai'i at Mānoa, 1000 Pope Road, Marine Sciences Building, Honolulu, HI 96822, USA.

7: Department of Biomedical Sciences, Copenhagen University, Blegdamsvej 3, 2200 Copenhagen, Denmark

8: Marine Biological Section, University of Copenhagen, Strandpromenaden 5, 3000 Helsingør, Denmark

9: Faculty of Health and Life Sciences, Linnaeus University, Kalmar, Sweden

10: Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

11: GEOMAR Helmholtz Centre for Ocean Research Kiel, Wischhofstr. 1-3,

24148 Kiel, Germany

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The size of an individual organism is a key trait to characterize its physiology and feeding ecology. Size-based scaling laws may have a limited size range of validity or undergo a transition from one scaling exponent to another at some characteristic size. We collate and review data on size-based scaling laws for resource acquisition, mobility, sensory range and progeny size for all pelagic marine life, from bacteria to whales. Further, we review and develop simple theoretical arguments for observed scaling laws and the characteristic sizes of a

change or breakdown of power laws. We divide life in the ocean into seven major realms based on their trophic strategy, physiology and life history strategy. Such a categorization represents a move away from a taxonomically oriented description towards a trait-based description of life in the oceans. Finally, we discuss life forms that transgress the simple size-based rules and identify unanswered questions.

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Introduction

Since the essay by Haldane (1928) "On being the right size" biologists have used organism size as a master trait to characterize the capabilities and limitations of individual organisms. There are good reasons for doing so. It is evident that the physiology and ecology of a copepod and a dolphin are vastly different, much more so than the difference between a copepod and a fish larva. Organism size describes individual physiology across major taxa through power-law functions (Peters 1983): metabolism, leading to the celebrated 3/4 law for the scaling of resting metabolism with size (Hemmingsen 1960, Kleiber 1932, West et al. 1997, Winberg 1956), population growth rates (Fenchel 1974, Gillooly et al. 2002), predator-prey relationships in terms of functional response (Hansen *et al.* 1997; Kiørboe 2011; Rall *et al.* 2012) and predator-prey ratios (Barnes et al. 2008, Cohen et al. 1993, Hansen et al. 1994), fluid-mechanical forces (Bejan & Marden 2006), swimming speed (Ware 1978; Kiørboe 2011), vision (Dunbrack & Ware 1987), diffusive uptake affinities (Aksnes & Egge 1991, Berg & Purcell 1977, Edwards et al. 2012, Litchman et al. 2007, Munk & Riley 1952, Tambi et al. 2009) and, for phytoplankton, affinities for light (Finkel 2001, Taguchi 1976) and maximum uptake rates (Edwards et al. 2012, Marañón et al. 2013). Size has also been used to describe macro-ecological patterns of size-dependent species diversity (Fenchel & Finlay 2004, May 1975, Reuman et al. 2014), and the biomass distribution of individuals as a function of size across major taxa (Boudreau & Dickie 1992, Sheldon & Prakash 1972) has been explained theoretically using the size relationships describing individual physiology (Sheldon *et al.* 1977; Andersen & Beyer 2006). While developing these size-

based relations the focus has been on determining the exponent (the “slope”) and the constant (“intercept”), with less attention being paid to the sizes that limits the range of their validity.

On closer inspection, some power-laws relationships are seen to change scaling exponent and/or intercept around some particular size or even break down altogether beyond a range of validity. The fluid flow around a whale, for example, is turbulent leading to dominance of inertial forces with a drag force scaling with the length and velocity squared. In contrast, the flow around a unicellular organism is laminar and dominated by viscous forces with a drag force scaling linearly with velocity and length. Consequently, the scaling of drag force changes at the organism size where there is a transition between viscous and turbulent flow. As example of a breakdown, consider the visual range. The larger the eye, the longer an organism can see. However, there is an upper visual range determined by the sensitivity of the retina (Dunbrack & Ware 1987), as well as a lower limit of eye size determined by the size of the visual elements in the retina and the wavelength of light. The scaling law for visual range is therefore valid only within the upper and lower limits. Such changes or breakdowns in scaling laws have consequences for adaptations and strategies of marine organisms. For example, predators so large that they are in the inertial fluid regime develop a streamlined body shape for efficient swimming and predators smaller than the lower size of an eye cannot rely on vision.

Haldane (1928) concluded that "*For every type of animal there is a most convenient size, and a large change in size inevitably carries with it a change of form"*. Our aim is to determine the sizes where scaling relationships change or break down and to use those characteristic sizes to explain the fundamental differences in the form and function of marine organisms with different sizes. To this end we build on the large existing literature of empirical size-based scaling relations and their theoretic explanations.

We categorize pelagic life in the ocean based on size in seven general realms: molecular life (viruses), osmo-heterotrophic bacteria, unicellular phototrophs, unicellular mixotrophs and heterotrophs, planktonic multi-cellular heterotrophs (e.g. copepods), visually foraging poikilotherms (e.g. fish), and homeothermic animals (whales). This categorization of life is a deliberately crude representation of the roughly 200,000 eukaryotic species, plus an unknown number of archea and bacteria, in the ocean (May & Godfrey 1994), as it is explicitly designed to facilitate an understanding based on size. We describe the life forms in each realm according to their body size and determine characteristic sizes where there is a transition from one realm to another. In this manner we emphasize body size as a fundamental driver of macro-ecological patterns in the oceans.

We examine five aspects of life where size is a dominant driver: (i) resource encounter through predation, diffusive uptake or photosynthesis, (ii) mobility, (iii) sensing through chemical and hydromechanical signals, vision, and

156 echolocation, (iv) life history strategy in terms of adult and progeny sizes and (v)
157 body temperature (
158 Figure 1). To this end we draw on a wide range of theories: diffusion theory, fluid
159 mechanics, optics, metabolic theory, and optimal life history theory. We review
160 established theoretical and empirical scaling laws and establish characteristic
161 sizes where the scaling laws change or break down. These characteristic sizes
162 are used to formulate hypotheses about the dominant strategy for organisms of a
163 given size within the five aspects, e.g. how an organism obtains carbon (through
164 photosynthetic assimilation of inorganic carbon, from dissolved organic matter,
165 or from particulate organic matter), or which senses it employs for prey
166 encounter. We test the hypotheses by collecting data on strategies of individuals
167 as a function of their size. Since our arguments are general in nature they apply
168 largely to all aquatic life but our focus is pelagic marine life. The final synthesis is
169 a description of the dominant forms and functions of life in the oceans. This is
170 used to frame a discussion of strategies and life forms that transcends the
171 general size-based patterns and to point towards open unanswered questions.

172 **What is 'size'?**

173 The size of an organism can be characterized by its length or by its weight. Wet
174 weight, dry weight and carbon weight are the most common weight measures,
175 while length is typically measured as the largest linear dimension or the
176 equivalent spherical diameter (ESD). Depending on the question one measure
177 may be more appropriate than the other. For example the flow around an
178 organism is determined by its linear size and shape, not by its weight.
179 Conversely, the bioenergetic budget of an organism is adequately described in

terms of weight since the energetic budget should reflect a conservation of mass. For microbes weight is often measured in carbon or in units of the limiting nutrients since water content and ratios between fundamental elements vary between organisms (Klausmeier et al. 2004). The elemental ratios and water content of vertebrates vary less than they do for invertebrates so wet weight is often preferred as an intuitive measure of weight for vertebrates. Even though it would be possible, we do not find it useful to convert all sizes to a common measure and consequently use the most convenient measure depending on the situation. We will use the symbols w for a weight and l for length, d for diameter and r for radius and frequently make use of the conversion between length and weight as $w \propto l^3$. Units of weight are indicated with subscripts: g_{WW}, g_{C}, referring to wet weight and carbon weight. Conversion relations are provided in Table S1.1.

Resource acquisition and trophic strategies

Organisms acquire carbon and nutrients through feeding on encountered resources. "Resources" is here understood broadly as dissolved inorganic nutrients, dissolved organic molecules, photons or prey organisms. The encounter with resources occurs by three mechanisms: 1) active encounter through cruising, ambushing or creation of a feeding current, 2) fixation of carbon through photosynthesis or, 3) passive encounter with food items which diffuse towards the feeding individual. The encounter rate (biomass per time) is described as:

$$E = \beta C \quad (1)$$

where β is the clearance rate (volume per time) and C the resource concentration (biomass per volume). In terms of a type II functional response (Holling 1959) the clearance rate is the slope at the origin i.e., the potential volume of water cleared for resources per unit time when uptake is not limited by handling time or physiological limits (digestion). These limitations are not considered here. The clearance rate is described as a power function of size $\beta = bl^a$. We employ the linear dimension l to characterize size because resource uptake is determined by the physical size of an organism, not by its weight. In the following we describe how the exponent a and the factor b depends on size for the three different resource acquisition mechanisms on the basis of physical processes and empirical cross-species relationships. This analysis allows us to characterize the dominant trophic strategy of organisms, e.g. phototrophs or heterotrophs, as a function of their size and the biotic and abiotic environment.

Active predation

Large protozoans and metazoans have three fundamental modes of actively encountering prey: ambushing, generating a feeding current or cruising through the water searching for prey (Kiørboe, 2011). The clearance rate of each mode β_A can be estimated as a velocity multiplied by an encounter cross section. A planktonic filter-feeder, for example, captures prey on its filter with a size scaling as the length of the organism squared l^2, with a feeding-current velocity $u \approx l^{0.8}$ (Huntley & Zhou 2004) leading to a scaling exponent of the clearance rate of

226 $a_A \approx 2.8$. Using similar arguments for the other feeding modes all lead to
227 exponents ≈ 2.8, i.e. slightly below 3, but multiplied by different factors (Kiørboe
228 2011). Since one feeding mode replaces the other depending on environmental
229 conditions and the size of the prey and the predator, the average life-form-
230 transcending scaling exponent becomes around 3 (
231 Figure 2a; Table S1.2):
232

$$\beta_A = b_A l^3$$

233
234 Weight-specific uptakes rates, $\propto \beta_A / w$, are therefore independent of size since
235 $w \propto l^3$ (Kiørboe & Hirst 2014).
236
237 *Photosynthesis*
238 Fixation of dissolved CO_2 by photosynthesis requires encounter with photons
239 (we assume that CO_2 is not limiting). Photosynthesis can in principle occur
240 throughout the cell but for larger cells it is limited by self-shading of photons
241 (the "package effect") (Morel & Bricaud 1981). For the present arguments, it is
242 sufficient to consider that the cross-sectional area of the cell $\propto l^2$ limits
243 photosynthesis (
244 Figure 2b):
245

$$\beta_L = b_L l^2 \quad (2).$$

246

The clearance rate β_L is often termed light affinity or photosynthetic efficiency and is measured in dimensions of carbon fixed per photon multiplied by area. In terms of weight specific scaling, the power 2 scaling of β_L results in a scaling of weight specific rates of carbon fixation $\beta_L/w \propto w^{-1/3}$, i.e. smaller organisms have a higher specific rate of carbon fixation than larger ones. Organisms smaller than a certain size are therefore able to fix more carbon by photosynthesis than by active encounter since specific uptake by active encounter is independent of size.

Diffusion feeding

Organisms that encounter resource items as they bump into the surface of the organism due to Brownian motion are termed "diffusion feeding" (Fenchel 1984). Diffusion feeding is used to assimilate dissolved organic molecules, inorganic carbon and nutrients. The uptake rate is limited by the number of uptake sites on the surface of the cell, which can be expected to scale with l^2. However, the uptake also removes resources from the vicinity of the cell surface and creates a boundary layer of lower resource concentrations near the cell than far away (Munk & Riley 1952). This effectively leads to the clearance rate β_D being limited rather by diffusion than by the surface, with a scaling proportional to the linear dimension of the cell (reviewed by Fiksen et al. 2013):

$$\beta_D = b_D l^1 \quad (3).$$

Weight specific uptake rates are then $\propto w^{-2/3}$, i.e., high for small cells and declining with size. Small diffusion feeding cells therefore have a higher encounter rate with dissolved nutrients or macromolecules than they could have obtained by active feeding. The theoretic scaling prediction fits with data for phosphate affinity (

Figure 2c). Data for nitrogen affinity are less clear, with some being consistent with the theoretic scaling ($a_D = 1.2$) (Litchman et al. 2007) and others not ($a_D = 2.25$) (Edwards et al. 2012).

Trophic strategies

An organism's trophic strategy, i.e., which type of food it consumes, is to a large degree determined by its resource acquisition mechanism. It can be an osmo-heterotroph that diffusion feeds on dissolved organic matter (bacteria), a phototroph that captures light and diffusion feeds on dissolved inorganic nutrients (phytoplankton), a mixotroph that captures light and feeds on other organisms, or an actively feeding heterotroph (animals and many protists). If we use clearance rate as a proxy for competitive ability at low resource concentrations, we can assume that the dominant trophic strategy of organisms at a given size is determined by the resource acquisition mechanism yielding the highest encounter rate. The encounter rates for the four trophic strategies as a function of size is given by Eq. 1 where the resource may be either concentrations of dissolved organic molecules C_{DOM}, nutrients C_N, other prey organisms C_P, or the light flux C_L. Phototrophs need special treatment since they assimilate inorganic carbon and nutrients by two different processes. Carbon is

assimilated through photosynthesis and combined with diffusively encountered nutrients to achieve a C/N ratio c_{CN}. The limiting compound determines encounter as described by Liebig's law of the minima:

$$E = \min\{c_{\mathrm{CN}} \cdot \beta_D \cdot C_N, \quad \beta_L \cdot C_L\}.$$

For a particular environment of light, nutrients, organic matter and prey, an organism encounters different specific amounts of resources from the various encounter mechanisms (

Figure 3). The smallest organisms get the highest encounter rate from diffusive encounter with dissolved organic matter. Diffusion feeding heterotrophic bacteria (osmo-heterotrophs) will therefore dominate among the smallest organisms. As size increases, encounter with photons becomes sufficiently high to make photosynthesis combined with diffusive uptake of inorganic nutrients optimal, i.e., the dominant strategy becomes phototrophy. The transition size is when carbon fixation by photosynthesis $\beta_L C_L = b_L l^2 C_L$ becomes equal to the diffusive encounter with dissolved organic matter $\beta_D C_{\mathrm{DOM}} = b_D l C_{\mathrm{DOM}}$, which occurs at a size:

$$l = \frac{C_{DOM} b_D}{C_L b_L} \ . \qquad (4)$$

Cells larger than this size are expected to be light-limited phototrophs. When the cells reach a size

$$l = \frac{c_{CN} C_N b_D}{C_L b_L} \quad (5)$$

315

316 the diffusive uptake of inorganic nutrients becomes limiting (Mei *et al.* 2009).
317 Larger cells will still benefit from acquisition of carbon through the aid of
318 photosynthesis but they will be nutrient limited. At a size

319

$$l = \frac{c_{CN} C_N b_D}{C_F b_A} \quad (6)$$

320

321 active encounter with prey organisms provides the highest encounter rates, i.e.,
322 heterotrophic animals. There is a particular range where photosynthesis will
323 provide more carbon than active encounter (predation) but where active
324 encounter provides more nutrients than diffusive uptake of inorganic nutrients.
325 In this size-range a mixotrophic strategy is profitable, i.e. using photosynthesis,
326 either from ingested or own chloroplast, predominantly to provide carbon for
327 metabolism, and using active feeding to assimilate nutrients and carbon for
328 biomass synthesis (mixotrophs of type II and III; Stoecker, 1998).

329

330 The size range where a certain trophic strategy gives the highest yield depends
331 on the concentration of available resources. If, for example, the concentration of
332 prey organisms is increased, the lower size limit where active feeding gives the
333 highest yield is decreased. The transition size between the dominant feeding
334 strategies will therefore be different under oligotrophic conditions (high light
335 and low nutrient concentrations, such as summer surface conditions in seasonal

336 environments or oceanic regions) than under eutrophic conditions (low light and
337 high nutrient concentrations, such as spring surface conditions in seasonal
338 environments or conditions at depth) (Figure 4a+b). The general pattern of small
339 diffusion feeders, medium phototrophs, and large active feeders is identical
340 between oligotrophic and eutrophic environments, but the sizes where the
341 transitions occur vary: oligotrophic conditions give rise to smaller phototrophs
342 and a large size-range of mixotrophs, while eutrophic situations conditions lead
343 to larger osmo-heterotrophic bacteria, phototrophs and mixotrophs. The general
344 pattern fits well with the classical interpretation of the seasonal succession of
345 cell size in temperate systems (Kiørboe, 1993): large (diatoms) cells dominate
346 during nutrient rich spring conditions but are overtaken by smaller cells
347 (dinoflagellates and cryptophytes), often with a mixotrophic strategy during the
348 nutrient depleted summer conditions (Barton *et al*. 2013).
349
350 A compilation of the dominant trophic strategies according to size largely
351 confirms the theoretical predictions while also highlighting the large overlap in
352 the size-range between phototrophs, mixotrophs and small heterotrophs (
353 Figure 4c). The overlap reflects that the compilation is based on the observations
354 from various environmental conditions that, as demonstrated above, create a
355 significant variation in the transition sizes where one trophic strategy gives a
356 higher yield than another strategy.

357 **Mobility**

358 Movement is powered by muscles or flagellae and constrained by friction from
359 the water. From an organism's perspective the nature of the water changes

360 dramatically with size: large organisms use their inertia to coast through the
361 water while smaller organisms experience water as thick and sticky. Very small
362 organisms have to cope with the random forces of molecules that induce
363 Brownian motion (Dusenbery 2009). The hydromechanics of movement can
364 therefore be divided into three regimes: an inertial regime, a viscous regime and
365 a Brownian regime. Here we are mainly concerned with the difference between
366 the inertial and viscous regimes. The hydrodynamic regime determines the
367 forces upon the body, which in turn influences the optimal shape. In the viscous
368 regime the dominating force is surface friction, which scales with the linear
369 dimensions of the body. In the viscous regime it is therefore optimal to reduce
370 the surface area, i.e. to be spherical (actually, the optimal shape is deviating
371 slightly from spherical; Dusenbery, 2009). In the inertial regime the drag force is
372 proportional to the projected frontal area of the organisms making it optimal to
373 reduce this area by streamlining..
374
375 Whether an organism is in the inertial or viscous regime depends on the
376 Reynolds number $Re = ul/\nu$ that describes the ratio between inertial and
377 viscous forces operating on a body of size l moving at velocity u through water
378 with kinematic viscosity $\nu \approx 10^{-2}$ cm^2/s. The crossover between the two
379 regimes is at $Re \approx 20 - 30$ (Webb 1988). The scaling of swimming velocity with
380 size in the two regimes differs: in the viscous regime the velocity was found
381 empirically to scale as $l^{0.79}$ (Kiørboe, 2011) while in the inertial regime theoretic
382 arguments predict a length scaling with exponents 0.42 (Ware 1978) or 0.5
383 (Bejan & Marden 2006); observation suggest a scaling $u \propto l^{0.45}$ (Figure 5a). The

empirical data indicate a crossover size between the viscous and inertial regime at body length of around 7 cm corresponding to a Reynolds number on the order of 1000. The relevance of size for body shape is evident (Figure 5b): small organisms do not appear constrained on their body shape, while fish and mammals are streamlined with an average aspect ratio around 0.25. Copepods are in between; they have a significantly larger aspect ratio than fish. During jumps, however, the Reynolds number becomes large thus giving them the advantage of a relatively slender body plan (Kiørboe et al. 2010).

Size and sensing

Actively feeding organisms perceive their prey by chemical or hydromechanical cues, vision, or echolocation. The range of sensing is determined by the size of the predator and the prey; a blue whale with an eye diameter of 15 cm sees much further than a fish larva with an eye diameter of 1 mm. The sense with the furthest range for organisms of a given size can be expected to dominate among organisms of that size. Organisms using more than one sense complicate the analysis of senses. For example, sharks use smell to follow the trail of a prey at great distances. When closing in on the prey, vision becomes important (Hueter et al. 2004). At distances below one meter they use electro-sensing for the precise localization of their prey (Collin & Whitehead 2004). Copepods are generally considered mechanosensing organisms, yet they can sense and follow the chemical trail of a settling marine snow particle (Kiørboe 2001) or the pheromone trail of a potential mate (Bagøien & Kiørboe 2005). Leaving such complications aside we nevertheless proceed to review estimates of the sensory

range of four senses where the sensing range depend on the size of the predator: chemical sensing, sensing of hydromechanical signals, vision and echolocation.

Chemosensing

In that all organisms depend on chemistry in one way or another, it may be safely assumed that they have machinery for chemical sensing. The question is how chemosensing together with behavior can bring organisms into contact with remote resources. The way organism's experience the coherence of chemical gradients and trails is determined by individual size in relation to turbulent eddies. Turbulence is characterized by three length scales (Tennekes & Lumley 1972): the Batchelor scale, ≈ 10 μm in the upper ocean, where turbulence starts to erode the regularity of a gradient, the Kolmogorov scale ≈ 1000 μm where turbulence starts to impede the organism's ability to maintain direction, and the integral scale $\approx$ 1-10 m where turbulent energy is injected by large-scale motions.

We distinguish between two modes of chemosensing: gradient climbing (e.g. bacterial run-tumble) and trail following (e.g. a shark following a prey trail). Gradient climbing relies on a chemical gradient set up by molecular diffusion of a solute from a source. The regularity of such gradients would be scale independent if it were not for turbulence. We can place an upper boundary for gradient climbing at between the Batchelor scale and the Kolmogorov scale, in the range from 10-1000 μm. Another limitation of the ability to follow gradients created by molecular diffusion is whether the trail is diffusing faster than the

movement of the prey. This criterion sets an upper limit for predator size of 50 μm (Kiørboe 2011). For trail following, additional criteria come into effect: the movement of the target organism, the rate at which it releases solute and how well the searching organism can detect this solute above background levels. In any case, organisms smaller than the energy containing turbulent eddies will experience the trail as patchy and therefore need to search large areas relative to their own size to follow the trail. This scenario is relevant for organisms of a size between the Kolmogorov and the integral length scales, i.e. organisms smaller than 1 m. Organisms larger than the integral scale are able to integrate over the subscale trail details and follow a trail without detours. Trail following is therefore most advantageous for large organisms and/or quiescent environments, e.g. the deep oceans (Martens et al.).

Mechanosensing

Ambush feeders may sense their prey via the fluid mechanical disturbance created by a moving prey (reviewed by Kiørboe 2011). To enhance the sensory range they employ special sensory arrangements protruding from the body, like the long setae-studded antennules on copepods or the sensory hairs arranged along the slender body of chaetognaths (arrow worms). The fluid mechanical disturbance of a self propelling prey can be modelled as a stress-let which implies that the signal attenuates as the cube of the distance away from the prey (Visser 2001). The range that this signal can be sensed is $R \approx \left(3\, l_{\mathrm{prey}}^2 l_{\mathrm{sensor}} u_{\mathrm{prey}}/u^*\right)^{1/3}$ where u^* is the detection limit of the velocity disturbance and l_{sensor} is the length of the sensor, approximately the size of the

predator. Using $u_{\mathrm{prey}} = b l_{\mathrm{prey}}^{0.74}$ and a predator-prey length ratio $B \approx 10$ the sensing distance is $R \approx c l^{1.24}$ with $c \approx 1.4\ \mathrm{cm}^{-0.24}$ for $u^* = 33\ \mu$m/s (Kiørboe 2011) (

Figure 6). An upper range comes into effect when the turbulent shear γ across the body of the predator organism approaches the sensitivity; i.e. when $u^* = \gamma l$. For moderate turbulent shears found in the upper ocean (0.03 s^{-1} which in the middle of the typical range of 10^{-4}-10^{-1} s^{-1}; Visser & Jackson 2004), this happens for l in the range 500-1000 μm. Mechanosensing is therefore most advantageous for small organisms (<1 cm) or on short ranges for large organisms.

Vision

Eyes contain photoreceptors that detect light and convert it into neuronal signals. The simple eyes of some microorganisms are only able to detect changes in the ambient light sufficient for detection of diurnal rhythms, orientation towards the surface and nearby movement. Active visual predation requires an eye with sufficient resolution to form an image and preferably also active optical machinery to focus a targeted object. With regards to feeding, the most important property of the eye is the distance at which it can discern a suitable prey.

[Sidebar 1 near here]

Dunbrack and Ware (1987) modelled the optical and sensing abilities of a camera eye to estimate the visual range of a predator of length l searching for

prey with a fixed fraction of the predator size (Sidebar 1). Two important conclusions emerge from their arguments: First, the sensing range scales as $l^{1.75}$ in clear water under high light conditions. Second the maximum range of large organism is limited by the optical properties of the water. Under perfect conditions the range is between 40-70 m (Davies-Colley & Smith 1995). The range decreases with the ambient light such that at depth, where the inherent contrast is low, visual range is mainly limited by the optical properties of the water.

A lower size limit of a functioning eye is determined by the finite size of the photoreceptor. Photoreceptors' functioning relies on opsin molecules (rhodopsin) stacked in rod cells with a width $d_{\mathrm{rod}} \approx 1\ \mu$m (Curcio et al. 1990). Taking account of the universality of the opsin design for photoreception, we may consider this length a limiting factor for building eyes. Considering a minimal resolution of, say 100^2 for sufficient image formation, results in a retina size of $d_r \approx 0.1$ mm. This is about $1/10$ of the size of the smallest aquatic organisms with camera eyes: larval fish and cephalopods. Therefore, vision is only a viable sensing mode for organisms in the size range from a few millimetres and up.

Echolocation

Echolocation is an active sensing mode, where the animal emits ultrasonic calls and interprets the environment based upon the echo of these calls. It is common

for toothed whales (Odontocetes) and while it is also used for orientation, here we focus on echolocation and its role in prey detection.

We can estimate how the range R of echolocation scales with the size of the animal based on three assumptions: 1) The sensitivity of the ear P_0 is independent of the size of the animal, 2) the emitted power scales with an exponent p as $P_e \propto w^p \propto l^{3p}$, 3) we ignore frequency dependent attenuation of sound in seawater because this attenuation is small compared to the conical spread of the sound wave. In free space the emitted signal spreads as a conic beam resulting in the attenuation of the signal power as R^{-2}. The power of the reflected signal is $P_r \propto P_e l_{\mathrm{prey}}^2 (2R)^{-2}$ where l_{prey}^2 is the area of the reflecting target and the factor 2 is because the signal attenuates both as it travels towards the target as well as when it returns. Inserting the power of the emitted signal and absorbing the factor 2 in the proportionality constant gives $P_r \propto l^{3p} l_{\mathrm{prey}}^2 R^{-2}$. The distance where the strength of the returned signal is just at the sensitivity of the ear, i.e. $P_0 = P_r$, scales as $R \propto P_0^{-1/2} l_{\mathrm{prey}} l^{3p/2}$. If the preferred prey size scales with the size of the predator, i.e. $l_{\mathrm{prey}} \propto l$, then:

$$R \propto P_0^{-1/2} l^{1+3p/2}.$$

If the power of the emitted sound follows metabolic scaling, $p = 3/4$ then the exponent becomes $17/8$. This argument only provides the scaling of the sensing range; the factor can be found by fitting to data (

Figure 6a).

Size and sense

The theoretic arguments outlined above identified three characteristic sizes where one sense becomes more efficient than another: 1) an upper size limit for gradient climbing at a predator size of around 100 μm; 2) predators larger than that 100 μm but smaller than 1 mm are expected to rely predominantly on hydromechanical sensing, 3) a size where vision becomes viable for a predators of around 1 cm, and 4) a size of around 1 meter or larger where predators are able to realize the upper visible range of up to 80 meter in clear water. An extension of the sensory range beyond this length can only be achieved by trail-following chemical tracers or by echolocation.

Analysis of body size and senses used by marine organisms reveals that the number of possible senses available to a predator increases with size (Figure 6b). Large organisms typically combine several senses for foraging. The lower size limit of vision around 1 cm is clearly borne out; this size indeed corresponds to the smallest size of fish and cephalopods larvae. Some large life forms do not use vision to detect prey, most notably the gelatinous zooplankton, even though they are much larger than 1 cm. Seen in this perspective, the strategy of gelatinous zooplankton is to avoid building a vertebrate body with its associated high metabolic requirements to utilize the increasing sensing range that vision provides but rather depend on an inflated body to increase the prey encounter cross section (Kiørboe 2013). The superiority of vision declines with

548 ambient light so the relative disadvantage of gelatinous zooplankton versus fish
549 diminishes in turbid water or in deep waters (Sørnes & Aksnes 2004).

550 **Life history and progeny size**

551 Though obvious on the individual level, the concept of size becomes ambiguous
552 when applied at the species level since all life differs in the size of adults and
553 progeny; even unicellular organisms need to double their size before they can
554 divide. The difference between adult and progeny size is most extreme among
555 the teleosts (bony fish) where the weight ratio between adults and larvae can be
556 up to 10^8 for bluefin tuna.
557
558 [sidebar 2 near here]
559
560 *Optimal life history theory*
561 The evolution of life history with a pronounced difference between adult and
562 offspring size can be understood from optimal life history theory (Andersen et al.
563 2008, Christiansen & Fenchel 1979). If we assume 1) standard metabolic scaling
564 of consumption $= Aw^n$ with $n \approx 3/4$ (West et al. 1997); 2) metabolic scaling of
565 mortality $\alpha A w^{n-1}$ (Andersen & Beyer 2006, Hirst & Kiørboe 2002, Peterson &
566 Wroblewski 1984); and 3) determinate growth, then the lifetime reproductive
567 output R_0 becomes (Sidebar 2):
568

$$R_0 = \frac{\epsilon}{2\alpha}\left(\frac{W}{w_0}\right)^{1-\alpha}, \qquad (7)$$

569

where W/w_0 is the ratio between the weight at maturation and weight of offspring, ϵ is the efficiency of reproduction and α is the physiological mortality, which is less than 1 (Andersen *et al.* 2008). Because the exponent $1-\alpha$ is positive R_0 is an increasing function of W/w_0. The metabolic assumptions thus predict an evolutionary pressure towards a life history with as large a ratio between adult size and offspring size as possible. Since no organisms has an infinite ratio between adult size and offspring size, a full understanding of what limits actual offspring size cannot be achieved from optimal life history theory based on metabolic scaling laws alone; the actual offspring size will be limited by other processes.

Offspring size strategies

Observed offspring size strategies employed by marine life can roughly be partitioned into two groups: a "fixed-ratio" strategy where offspring size is a constant fraction of the adult size and a "small-eggs" strategy where offspring size is the same, independent of adult size (Neuheimer et al.) (
Figure 7). Crustaceans, cartilaginous fish and whales employ the fixed-ratio strategy with an adult:offspring weight ratio around 100:1. The metabolic optimal life history theory (eq. 7) is unable to predict the fixed-ratio strategy. For marine mammals the fixed-ratio strategy can be explained by the need to perform parental care (Shine 1978). For the other groups, the fixed-ratio strategy can be explained by an elaboration of the evolutionary argument in sidebar 2, to account for density dependent effects (Olsson et al.). Such elaboration shows that the strategy that maximizes W/w_0 is only optimal if the

offspring do not experience density dependent effects right at the time of hatching. If they do experience density dependent survival early in life, an evolutionary stable strategy with $W/w_0 \approx 100$ emerges.

Transitions between life forms

We have reviewed how size influences resource acquisition, mobility, ability to sense prey, and life-history strategy, based on theoretical arguments and cross-species empiric analyses. We now use these relations to understand the mechanisms behind the transitions between the seven realms of marine life: molecular life, osmo-heterotrophic bacteria, unicellular phototrophs, unicellular mixotrophs and heterotrophs, planktonic multi-cellular heterotrophs with ontogenetic growth, visually foraging poikilotherms, and homeothermic animals (

Figure 1 and Table 1). These seven realms correspond to the traditional taxonomic division of life between viruses, bacteria, phytoplankton, uni- and multicellular zooplankton, fish and marine mammals. Our alternative naming reflects the function of the groups and highlights the factor that determines the characteristic size where there is a transition between the groups.

A central theme is that development of larger size opens new possibilities for resource acquisition and sensing. Examples are how the battery of available senses increases with size (

Figure 6), how the emergence of multicellularity makes it possible to increase the adult:offspring size ratio and thereby increase fitness (Sidebar 2), or how mortality decreases with size. Larger size therefore increases the competitive

edge, provides access to new resources as well as increases survival. The sizes where new possibilities appear often mark a transition between the major life forms because the utilization of new senses etc. require fundamental changes in body plan and life strategy.

From viruses to cells

The smallest size of a cell is around 10^{-15} g_C with a diameter around 0.1 – 1 μm. Organisms this small are believed to be functionally limited by metabolic constraints (Kempes et al. 2012) and the size of non-scalable components: genome size (DeLong et al. 2010) and in particular the cell wall (Raven 1994). The wall size along can be used to calculate a lower limit for cell size: The wall has a mass $c_{\mathrm{wall}}d^2$ and the cell itself cd^3 where c_{wall} and c are constants. If we ignore the genome a theoretical lower limit to cell size is when all cell mass is used by the wall:

$$d_{\mathrm{limit}} = \frac{c_{\mathrm{wall}}}{c} \quad (8)$$

For a 0.5 μm cell the wall comprises abound 30 % of the total mass (Raven 1994), so $c_{\mathrm{wall}}/\mathrm{c} \approx 0.3{\times}0.5$ μm. This gives a lower limit cell size of $d_{\mathrm{limit}} \approx 0.15$ μm.

From osmo-heterotrophs to phototrophs

The smallest unicellular organisms are heterotrophic bacteria feeding on dissolved organic matter encountered through diffusion. At a diameter

641 $C_{\mathrm{DOM}} b_D/(C_L b_L)$ (eq. 4), it becomes favourable to fix inorganic carbon through
642 photosynthesis instead of relying on dissolved organic matter. This size depends
643 on the relative concentrations of dissolved organic matter C_{DOM} and light C_L, but
644 it can be as small as 10^{-14} g_C in the upper photic zone with concentrations of
645 dissolved organic matter $C_{\mathrm{DOM}} \approx 5\ \mu g_C/l$ and abundant light ($C_L \approx 7$ J day^{-1}m^{-2})
646 and increases as a light decreases (
647 Figure 4).
648
649 *From phototrophs to heterotrophs*
650 The smallest phototrophs are expected to be carbon limited (which in practice
651 means that they are limited by the amount of light since dissolved inorganic
652 carbon is assumed to be plentiful), while the largest phototrophs are expected to
653 be nutrient limited. This difference emerges from the different scaling of nutrient
654 encounter that scales with l^1 and light encounter that scales with l^2 (Eqs. 2 and 3
655 and
656 Figure 3). As before, the exact sizes where the transitions between light limited
657 phototrophs, nutrient limited phototrophs, and heterotrophs occur depend on
658 the specific conditions of dissolved nutrients, light and suitable prey (Figure 4b).
659 An order-of-magnitude estimation of the characteristic transition between
660 phototrophs and pure heterotrophs is 10^{-7} g_C ($l \approx 6\times10^{-2}$ cm), but it can vary
661 between 10^{-8} g_C in low light and high nutrients situations and 10^{-5} g_C in
662 situations of high light.
663

664 The size that marks the transition between phototrophs and heterotrophs is
665 blurred by a large group of mixotrophic organisms that acquire nutrients and
666 carbon for biomass synthesis from phagotrophy while photosynthesis primarily
667 provides carbon for metabolism. The mixotrophic strategy is most favourable for
668 organisms with sizes in the transition between phototrophy and heterotrophy.
669 The size range where the mixotrophic strategy is favourable varies with
670 environmental conditions: it is vanishingly small in eutrophic conditions and
671 increases to more than a factor 10 in diameter in oligotrophic conditions, in
672 agreement with observations (Barton et al. 2013).
673
674 *Unicellular to multicellular life*
675 The drive to develop larger size eventually leads to multicellular organisms.
676 Multicellularity opens the possibility of specialized tissue for, e.g., sensory
677 organs. Among microscopic metazoans the dominant group of copepods has
678 developed sensory apparatus to detect prey via hydromechanical cues and
679 appendages to generate feeding currents and make jumps to escape predators.
680 We have not developed a specific argument for the size where the transition to
681 multicellularity occurs, but since life-history theory predicts that increasing
682 offspring-adult size ratio increases lifetime reproductive output (Eq. 7), it is
683 likely to occur at the smallest possible size. DeLong *et al.* (2010) argue that this is
684 when it becomes possible to develop a fractal delivery network, around 10^{-6} g_C
685 (≈ 1 μm). The drive towards minimization of offspring and maximization of
686 adult size means that each metazoan group strives to extend its size range, but is

687 only able to do so within the limits defined by the sizes where there is a
688 breakdown in a scaling relationship describing a vital function.
689
690 *From copepods to fish*
691 Fish (including cephalopods) are the dominant organisms in the size-range from
692 1 mg_{WW} to about 100 kg (1 cm to 2 m). Fish are characterized by being
693 streamlined, visual predators. At a size smaller than 1 mg_{WW} the dominating
694 organisms are blind copepods, with a very non-streamlined body plan. The
695 transition size between these two very different life forms is characterized by the
696 transition from the superior sensing mode being mechanosensing to vision and
697 the transition from a viscous to an inertial hydromechanical regime. The change
698 in hydromechanical regime explains the slender fish shape, but it also entails a
699 change in feeding mode. Fish larvae employ suction feeding, which becomes
700 increasingly difficult the smaller they are (China & Holzman 2014). Probably the
701 most important transition is in sensing, with the lower size limit of fish
702 coinciding with the lower size of a functioning eye. Were fish to make smaller
703 eggs their larvae would be unable to compete with the tactile sensing copepod
704 with a morphology designed for optimal movement and prey capture in a viscous
705 fluid environment; were copepods to become larger they would be outcompeted
706 by visually sensing fish with streamlined bodies.
707
708 *From fish to whales*
709 Whales are the largest organisms in the oceans, occupying the size range from
710 about 100 kg and up. It is tempting to attribute the transition from fish to whales

711 to the appearance of echolocation as a possible sensing mode. However, only
712 toothed whales employ echolocation for sensing, whereas baleen whales rely on
713 the same senses as fish. If there are no change in the power law relationships
714 determining sensing and food encounter, why, then, have teleosts not evolved
715 even larger sizes than the few hundred kilos of the largest fish (bluefin tuna or
716 sunfish with maximum weights of 450 and 1000 kg_{WW})? We propose two
717 arguments for the transition between fish and marine mammals: a metabolically
718 based upper limit of a water-breathing organism (Freedman & Noakes 2002;
719 Makarieva et al. 2004, Supp.) and a lower size limit of a homeothermic (warm-
720 blooded) organism.
721
722 We have focused on acquisition of resources in terms of carbon and nutrients,
723 but heterotrophs also need oxygen to fuel their metabolism. The absorption of
724 oxygen through gills is limited by the surface of the gills. Since the surface of gills
725 is fractal it will scale with an exponent between 2/3 and 1, probably very close to
726 the metabolic exponent of 3/4. The acquisition of oxygen therefore scales with a
727 similar exponent as metabolism, so the relative ability to acquire food and
728 oxygen is independent of size. However, larger organisms accumulate heat
729 created by activity and use this to elevate their metabolism. Notable examples
730 are the scombroids (tuna and marlin) and pelagic sharks (Block 1991). A high
731 body temperature means higher activity and therefore higher predatory success
732 against slower heterothermic (cold-blooded) prey. Such an increase in
733 metabolism will eventually require more oxygen than can be obtained by
734 pumping water over the gills. This problem is solved by ram ventilation, which

735 provides a higher flow of water around the gills and therefore a higher oxygen
736 absorption rate. Evidence for this is provided by the largest fish being either very
737 active ram-ventilating (large scombroids or sharks) or relatively sluggish
738 pumping (sunfish). We conjecture that it would be impossible for fish to develop
739 homeothermy as a means of competing with marine mammals; the solubility of
740 oxygen in water is simply too low to fuel a homeothermic metabolism. Marine
741 mammals fuel their high homeothermic metabolism by breathing air, which has
742 a much higher solubility of oxygen than water.
743
744 For homeotherms the loss of body heat should be included in the energy budget
745 as this defines a lower limit for the size of a homeotherm (Haldane 1928). Heat
746 loss is a surface process that scales as $\propto \kappa w^{2/3}$ where κ is the thermal
747 conductivity of water. Since organisms wish to minimize heat loss their surface is
748 not fractal and the exponent is not larger than 2/3. The energy for heating comes
749 from the acquisition of resources (oxygen and food), which scales metabolically
750 as $Aw^{3/4}$. The size where there is a balance between loss of heat and acquisition
751 of resources defines a lower limit of homeothermy as $(A/\kappa)^{12}$ (Andersen et al.
752 2008). This lower limit is very sensitive to the value of the parameters A and κ
753 since their ratio is raised to a high exponent. For example, the ratio between the
754 lower limits calculated for a marine and a terrestrial habitat is the ratio between
755 the heat conductivity in air and water (≈ 20), raised to power 12 which gives
756 4×10^{15}. This factor is much larger than the ratio between the smallest whale, a
757 harbour porpoise calf of around 10 kg, and the smallest terrestrial homeotherm,
758 an Etruscan shrew (*Suncus etruscus*) at around 0.1 g. Nevertheless it seems

759 evident that the smallest land animals are limited by loss of heat, e.g. shrews
760 huddle together to conserve heat, so how can whales manage to attain a small
761 size in the face of a larger heat loss? We hypothesise that whales do that by
762 having an insulating layer of blubber. To achieve a lower size of 10 kg (a factor
763 10^6 smaller than predicted), whales need to decrease heat losses by a factor
764 $10^{6/12} \approx 3.2$ relative to terrestrial animals, which is not out of scope.

765 **Beyond size**

766 We posit that individual size is the most important trait characterizing a pelagic
767 organism. Knowing the size, it is possible to estimate, often within an order of
768 magnitude, the metabolic rate, the clearance rate, the swimming speed and the
769 sensory range. We have shown how that information facilitates inference of
770 trophic strategy, sensory mode, body shape, and, to some degree, reproductive
771 strategy. Though important, we have largely ignored the subtle interplay
772 between temperature, oxygen concentration and size (Verberk & Atkinson
773 2013). Even though size can be characterized as a "master trait" (Litchman &
774 Klausmeier 2008), it is not the only trait that characterizes an organism. The
775 relevant question is then which other traits best characterize the variation
776 around the mean in the reviewed relations with size (
777 Figure 2, 5 and 7). We propose three candidate traits to consider: predator-prey
778 size ratio, "feeding mode" for heterotrophic metazoans and "jellyness".
779
780 Among heterotrophic metazoans there appear to be two dominant strategies to
781 predator-prey size ratio: a fixed predator-prey length ratio in the range 10-100,
782 which is the strategy followed by most fish and copepods (Barnes et al. 2008), or

783 a strategy aimed at preying on organisms much smaller than the predator. The
784 small-prey strategy is used by the largest zooplankton, the pelagic tunicates, and
785 by the largest vertebrates, the whale sharks and the baleen whales. Organisms
786 with a large predator-prey size ratio rely on filtering the water to catch the prey.
787 It is presently unknown what drives the development of the two alternative, but
788 apparently equally competitive, strategies.
789
790 The feeding mode determines whether an actively feeding predator encounters
791 its prey through ambushing or cruising. It is often assumed that predation
792 pressure is a function of size only and therefore independent of feeding strategy
793 or sensing mode. This is not quite true. It is becoming increasingly evident that
794 feeding strategy is associated with a trade-off in mortality: an ambush feeder will
795 encounter less prey than a cruising predator but it will also have less exposure to
796 predation and therefore lower mortality. A quantitative demonstration of this
797 trade-off has been made for zooplankton based on laboratory experiments
798 (Kiørboe 2013b) and the importance for the seasonal succession has been
799 modelled (Mariani et al. 2013). These trade-offs likely apply at least qualitatively
800 to other predators, e.g. fish.
801
802 A related trade-off is the development of a gelatinous body (jellyfish, box jellies
803 and pelagic tunicates). We argued in section “sensing” that visual predators
804 would be superior to predators sensing their prey through hydromechanical
805 forces. However, the inflated body size of gelatinous organisms results in a large
806 encounter cross-section and hence a higher clearance rate than a non-gelatinous

organisms with the same carbon body mass. This is what makes the jelly-strategy effective even in the same size range where visual predation is possible (Acuña *et al.* 2011), particularly under low light conditions (Sørnes & Aksnes 2004). At the same time the gelatinous body makes the organism less attractive to predators thereby lowering its mortality. These two examples show how the general ”rules” inferred from size scaling of encounter, mobility, and sensing can be transgressed by other traits.

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Acronyms and definitions

Power law: $y = ax^b$ with factor a and exponent b. Linear regression employs a logarithmic transformation: $\log y = \log a + bx$, with $\log a$ being "intercept" and b the "slope".

Poikilotherm: An organism that maintains the same body temperature as the environment, in contrast to a **homeotherm** which maintains a constant body temperature due to internal heat sources.

Protists are simple, typically unicellular, eukaryotic organisms, living in aquatic environments.

An organisms' **trophic strategy** describes how it gathers nourishment. The suffix "troph" derives from ancient greek: *trophe*=food, nourishment; *drepo*=to gather.

Phototrophs rely on photosynthesis as their carbon source and use **osmotrophic** diffusive uptake of nutrients. In contrast **phagotrophs** up carbon and nutrients by absorbing other living organisms. **Mixotrophs** employ a mixed strategy, typically combining photosynthesis with phagotrophy.

Note for production: The above definition is longer than 20 words (37), but it also defines four terms.

Cartilaginous fish (*Chondrichthyes*) are fish with skeletons made of cartilage rather than bone, containing elasmobranchs (sharks, rays and skates) and Holocepahlii ("ghost sharks").

Cephalopods are squid, octopi and cuttlefish, commonly referred to as "inkfish".

The **physiological mortality** is the ratio between mortality and weight-specific consumption. With metabolic scaling of uptake $Aw^{3/4}$ and mortality $cw^{-1/4}$ the physiological mortality becomes $\alpha = c/A$.

Stresslet: A stokes flow produced by 2 co-linear anti-parallel point forces acting on a fluid.

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1036 Table 1. Characteristic sizes of transitions between major realms of life in the

1037 ocean.

Transition	Size	Notes
Lower size of a cell	0.15 μm $\approx 10^{-15}$ g_C	Limited by cell wall and to a lesser extent genome size (Eq. 8)
Osmo-heterotrophs to phototrophs	10^{-14} to 10^{-13} g_C	Transition from diffusion feeding on DOM to photosynthesis (Eq. 4).
Phototrophs to mixotrophs	10^{-8} g_C	Transition from acquiring inorganic nutrients by diffusion feeding to acquiring nutrients by active feeding (Eq. 5)
Mixotrophs to heterotrophs	10^{-7} g_C (10^{-8} to 10^{-5} g_C)	Acquisitions of carbon and nutrients solely by predation through active feeding (Eq. 6)
Single- to multicellular organisms	10^{-6} g_C	Development of vascular networks.
Copepods to fish	$\approx$ 1 mg_{WW}	Smallest size of a functional camera eye
Fish to whales	$\approx$ 10 kg_{WW}	Lower size of maintaining a homeothermic metabolism

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Sidebar 1: The Dunbrack and Ware model of visual range

The maximum visual range in clear water can be estimated by considering the properties of a pin-hole camera eye as done in a largely unrecognized work by Dunbrack and Ware (1987). Here we provide a simplified derivation of their argument, which corrects a number of minor errors.

The projection of a visual image of a prey on the retina of a predator activates a number of visual elements n proportional to the area of the projected image multiplied by the density of visual elements. Since we are interested in the maximum distance R that an object can be discerned we can assume that the distance is large relative to the diameter of the eye such that the curvature of the eye can be ignored. The number of activated visual elements is: $n \propto \rho l_{\text{eye}}^2 l_{\text{prey}}^2 R^{-2}$ where ρ is the density of visual elements and l_{eye} is the diameter of the eye. The density of visual elements is a decreasing function of the size of the eye: $\rho \propto l_{\text{eye}}^{-d}$ with $d \approx 0.5$ (Dunbrack & Ware 1987). Assuming that the size of the eye and the preferred size of the prey scales with the length of the predator gives the number of visual elements as

$$n \propto l^{4-d} R^{-2}.$$

The largest distance R that a predator can discern a prey of size (length) l_{prey} is when the apparent contrast (the difference between the visual imprint of the prey and the background) of the prey C_a equals the contrast threshold that the predator can distinguish C_t. Apparent contrast of the prey declines away from the

inherent contrast $C_0 = 0.3$ as:

$$C_a = C_0 e^{-\alpha R}.$$

Where $\alpha = 0.001$ cm^{-1} is the attenuation of light by the water. The contrast threshold is a declining function of the number of visual elements n involved in discerning the object:

$$C_t = C_{t.\min} + 1/n$$

where $C_{t.\min} = 0.15$ is the minimum contrast threshold for vision which depends on the ambient light. This semi-heuristic relationship is known as "Ricco's law" (Northmore et al. 1978). The maximum distance where the prey can be perceived is when the apparent contrast reaches the contrast threshold, $C_a = C_t$:

$$C_0 e^{-\alpha R} = C_{t.\min} + KR^2 l^{d-4}$$

where $K = 0.025$ cm$^{1.5}$ is a constant which characterizes the sensitivity of the eye. It is not possible to isolate R from the expression above. However, two limiting cases can be derived: 1) the "clear-water" limit is when the visual range is limited by the resolution of the eye, i.e. where $e^{-\alpha R} \approx 1$ and $C_0 \gg C_{t.\min}$:

$$R \approx \sqrt{C_0/K}\, l^{2-d/2}$$

In this case the maximum visual range increases with $l^{2-2/d} \approx l^{1.75}$ for $d = 0.5$. 2)

The "turbid-water" limit is when the visual range is limited by the sensitivity (the minimum contrast threshold) of a visual element, when $C_{t.\min} \gg KR^2 l^{4-d}$:

$$R \approx \frac{\ln C_o - \ln C_{t.\min}}{\alpha}$$

In this limit the size of the predator does not play a role and the minimum contrast threshold essentially limits the visual range. The visual range decreases if the light in the water is limited (lower minimum contrast threshold $C_{t.min}$) or the turbidity α is increased. The prediction of this limit has been subject of more elaborate models (Aksnes & Utne 1997).

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Sidebar 2 Life-history optimization of offspring size

The optimal life history strategy in terms of offspring size and adult size is the strategy that maximizes lifetime reproductive output (Charnov 1993). In optimal life history theory lifetime reproductive output is determined by the mortality and the available energy as functions of size or age. Here we determine the offspring size which maximizes lifetime reproductive out using arguments from Christiansen & Fenchel (1979) and Andersen *et al.* (2008).

The available energy can be assumed from metabolic scaling arguments to be $H(w) = Aw^n$ where the usual metabolic assumption is $n = 3/4$ (West et al. 1997). Consumption results in a mortality on their prey of $\mu(w) = \alpha w^{n-1}$ where α is a dimensionless constant relating consumption and mortality (Andersen & Beyer 2006). For simplicity we assume determinate growth where a juvenile uses all acquired energy for growth and a mature individual of size W uses all energy for reproduction; however the central results are valid for indeterminate growth as well (Andersen et al. 2008). The lifetime reproductive output (expected number of offspring during life) is:

$$R_0 = \frac{\epsilon}{2} P_{w_0 \to W} \frac{H(W)}{w_0 \mu(W)}$$

where ϵ is the reproductive efficiency, ½ assumes an even sex ratio, $H(W)$ is the adult rate of reproduction (mass per time), $1/\mu(W)$ is the expected adult lifespan, $1/w_0$ is to convert from units of mass to number of offspring, and the probability

to survive from offspring size w_0 to adult size W is:

$$P_{w_0 \to W} = \exp\left[-\int_{w_0}^{W} \frac{\mu(w)}{H(w)} dw\right]$$

Inserting the metabolic assumptions, $H(w) = Aw^n$ and $\mu(w) = \alpha A w^{n-1}$ yields a lifetime reproductive output of:

$$R_0 = \frac{\epsilon}{2\alpha}\left(\frac{W}{w_0}\right)^{1-\alpha}$$

Three conclusions can be drawn from this result:

1) If $R_0 < 1$ each female produces less than a single offspring throughout life yielding an unsustainable population. This happens when $\alpha > 1$ and it can be concluded that $\alpha < 1$.

2) Lifetime reproductive output only depends on the ratio between adult size and offspring size. The absolute values of the two sizes do not matter.

3) The larger the ratio between adult and offspring size, the higher the fitness. Organisms will therefore strive to maximize this ratio under the constraints of other external factors (Neuheimer et al.).

The results do not depend on the value of the metabolic exponent n as long as $n < 1$. This argument ignored the maintenance metabolism and indeterminate growth to simplify the mathematical derivation, but both of these effects can be

accounted for (Andersen et al. 2008).

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Figures

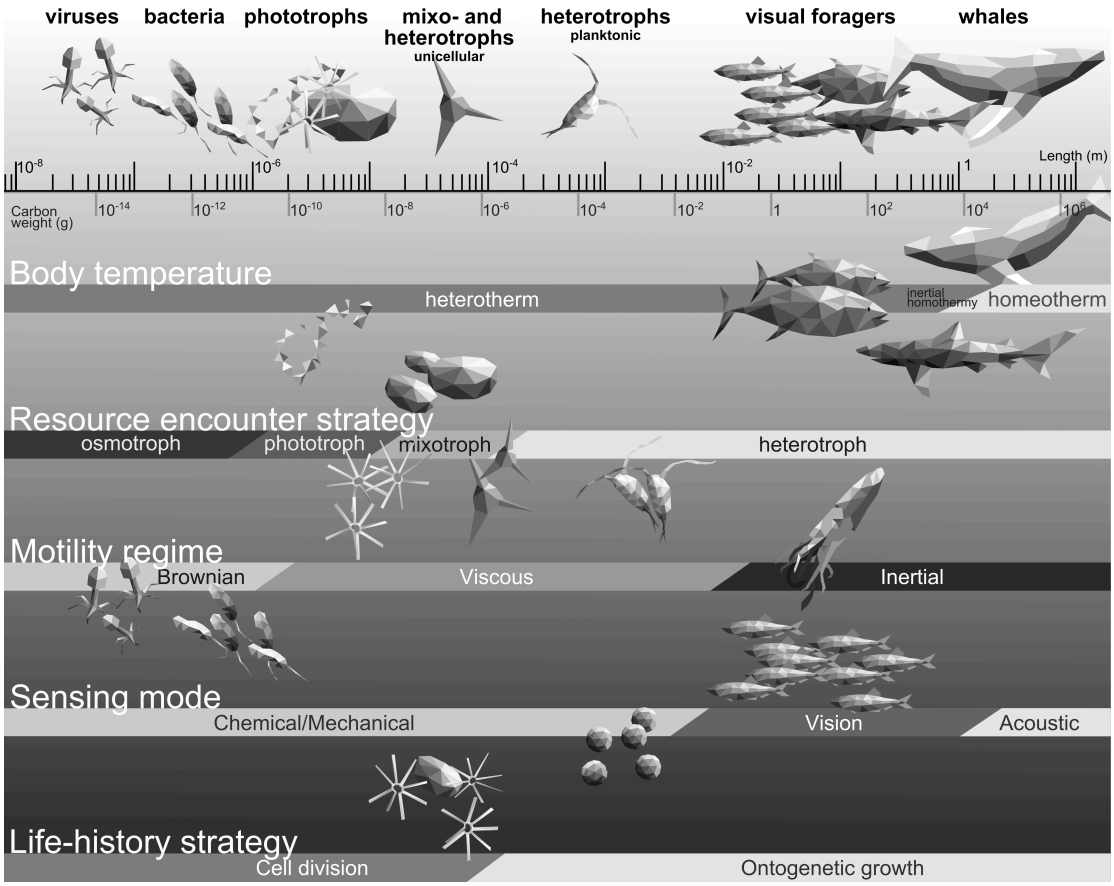
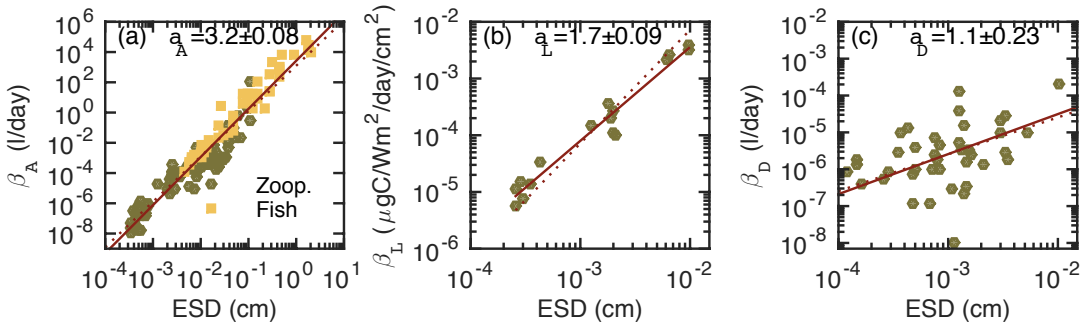


Figure 1. The five aspects of pelagic marine life examined here (body temperature, resource encounter strategy, motility regime, sensing mode and life-history strategy) are illustrated with horizontal bars with the characteristic transitions indicated by changes in gray-scale. The transitions are explained throughout the text. The drawings in the top row illustrate the seven realms of life: viruses, osmo-heterotrophic bacteria, unicellular phototrophs, unicellular mixo- and heterotrophs, planktonic multi-cellular heterotrophs, visually foraging poikilotherms (teleosts, cephalopods and sharks) and homeothermic animals (whales).



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1058 Figure 2. Clearance rate vs. weight for organisms performing active predation,
1059 photosynthesis and diffusive feeding on phosphorous. The solid lines are fits to
1060 data with exponent given in each panel. The dashed lines are fits with theoretical
1061 exponents 3, 2 and 1 for panel a, b and c respectively (Table S1.2). (a) Clearance
1062 rate β_A for active predation by zooplankton (circles) and fish (squares) from
1063 Kiørboe (2011). (b) Clearance rate β_L (affinity) for carbon uptake from a series
1064 of experiments with diatoms under identical conditions (Taguchi 1976). Data
1065 compilations covering a wider range of sizes and phytoplankton groups give a
1066 similar exponent but a larger scatter (Schwaderer et al. 2011). (c) Clearance rate
1067 β_D (affinity) for diffusive feeding on dissolved phosphate from Tambi et al.
1068 (2009) and Edwards et al. (2012).

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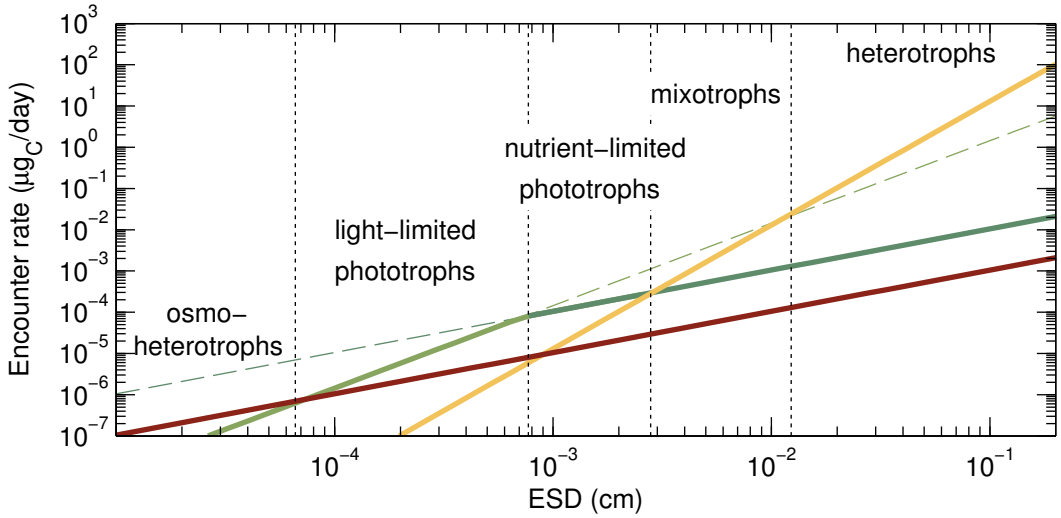


Figure 3. Encounter rates as a function of size for four different resource acquisition mechanisms and resource types: diffusive uptake of dissolved organic matter scaling as l^1 (dark red), uptake of carbon through photosynthesis scaling as l^2 (light green), diffusive uptake of dissolved inorganic nutrients (dark green), and active encounter of prey organisms scaling as l^3 (yellow). The combined uptake of carbon and nutrients by phototrophs is limited by Liebig's law and shown with solid green lines; light green for light-limited conditions and dark green for nutrient-limited conditions. The concentration of dissolved organic matter is $C_{\mathrm{DOM}} = 5\ \mu\mathrm{g_C/l}$; inorganic nutrients is $C_N = 4\ \mu\mathrm{molN/l}$ (corresponding to 50 $\mu\mathrm{g_C l^{-1}}$), the light intensity at depth is $C_L = 2$ W m^{-2} and the concentration of suitable prey organisms is $C_P = 10\ \mu\mathrm{g_C/l}$.

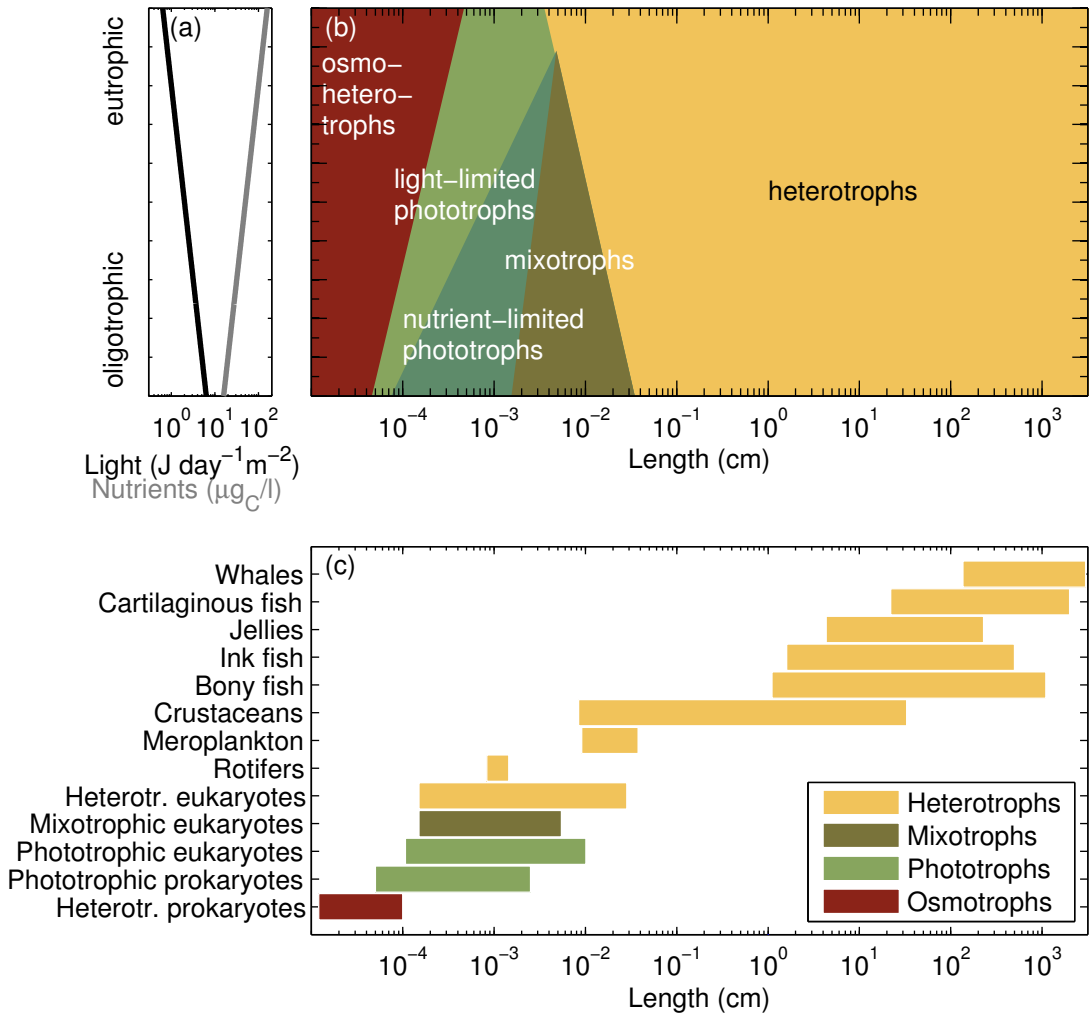


Figure 4. Trophic strategy as a function of size: osmo-heterotrophs (dark red), phototrophs (green), mixotrophs (army green) and heterotrophs (yellow). (a) Prescribed variation of nutrient and light conditions from oligotrophic to eutrophic conditions. (b) Strategy that yields the highest resource encounter rate as a function of size (x-direction) and resource condition (y-direction) changing between oligotrophic (high light, low nutrients) to eutrophic conditions (low light, high nutrients). (c) Trophic strategy of 3020 marine organisms as a function of length. Ciliates and flagellates have been categorized as phototrophs, mixotrophs or heterotrophs depending on the trophic strategy for the specific species (Appendix S2 in Supporting Information). The groupings are whales

(Cetacea only, i.e. dolphins and whales), cartilaginous fish (Elasmobranchii; sharks and rays), teleosts (Osteichthyes), Cephalopoda ("ink fish"), meroplanktonic larvae (i.e. planktonic larvae whose adult stages are benthic), jellies (Cnidaria, Ctenophora), rotifers (Rotifera), crustaceans (incl. copepods), and unicellular eukaryotes or prokaryotes.

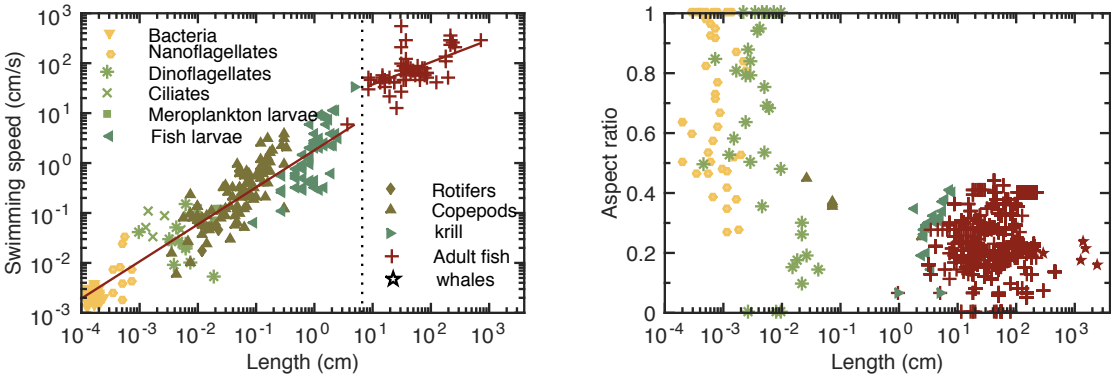


Figure 5. Swimming speeds and body aspect ratio vs. body length. Length is measured as ESD for planktonic organisms and as longest length for fish larvae, krill, fish and whales. (a) Swimming speed: data for zooplankton (including fish larvae) from Kiørboe (2011); fish data (cruising speed) from Sambilay Jr. (1990). The lines are power law fits (Table 1). The split between the two data sets was determined as the size that gave the lowest total residual of the fits. The crossover size at 6.6 cm corresponds to a Reynolds number around 1000. (b) Aspect ratio as a function of length for motile marine organisms. Data contain nanoflagellates and dinoflagellates (Throndsen et al. 2003, Tomas 1997), copepods (Kiørboe et al. 2010), krill (Watkins & Brierley 2002), fish larvae (Ara et al. 2013, Morioka et al. 2013, Moser et al. 1986, Oka & Higashiji 2012) and adult fish (Froese & Pauly 2013).

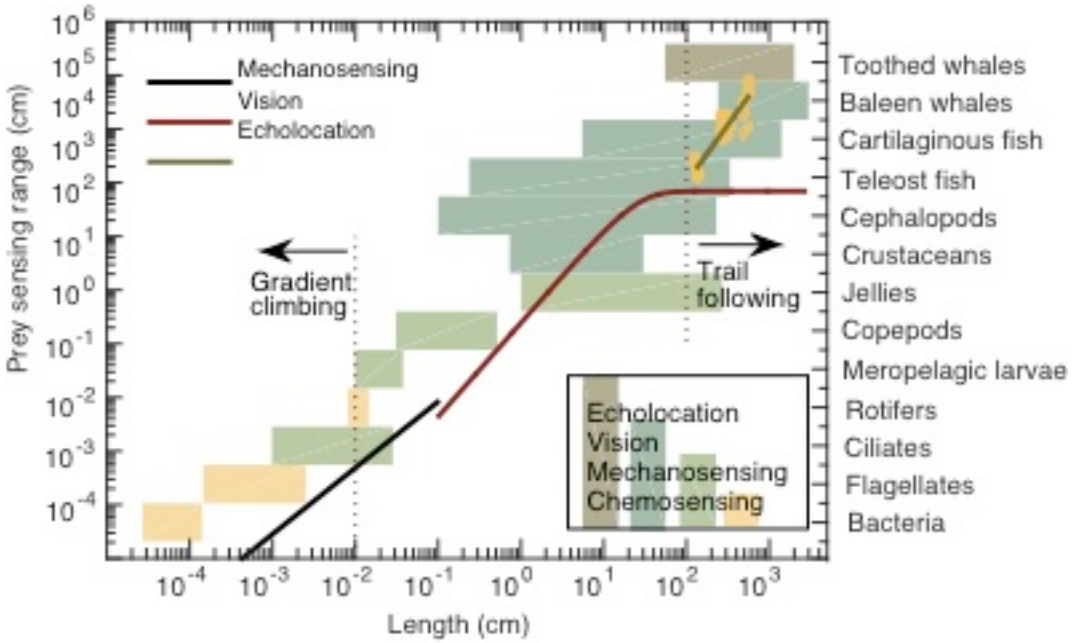
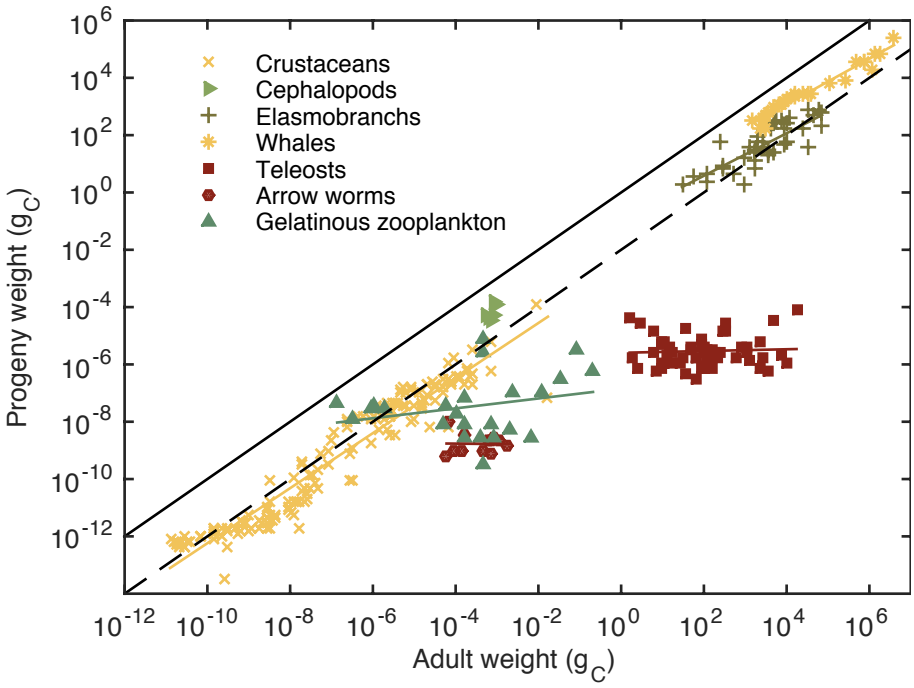


Figure 6. . Senses vs. size. Left axis and lines: Estimated range for sensing a prey a factor 10 shorter than a predator. (see Sidebar 1 for details). Echolocation range determined from tank and field measurements of tooth whales of different size (circles; Table S3.2). The line is fitted with exponent 17/8 (table 1). The vertical lines are estimates of limits of chemotaxis strategies; see text for details. Right axis and bars: Senses used for detecting prey grouped according to size and organismal group (Table S3.1).



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1130 Figure 7. Weights of adults and progeny for metazoans grouped by species of
1131 similar taxonomy. Estimates of mean adult and progeny size were compiled from
1132 the literature, with "adult" defined as individuals that had reached maturity and
1133 "progeny" the smallest size at which offspring are independent of the parent
1134 (Appendix S4). Original data included measures of volume, length, wet weight,
1135 dry weight and carbon dry weight. All were converted to carbon dry weight
1136 using either species-specific or, if unavailable, group-specific conversion factors
1137 from the literature. The solid line is a 1:1 progeny:adult size ratio and the dashed
1138 line is a 1:100 progeny:adult size ratio. Life forms following this line (whales,
1139 cartilaginous fish and crustaceans) follow the "fixed-ratio" strategy, while life
1140 forms with constant progeny size (most notably teleost fish) follow the "small-
1141 eggs" strategy.

1142