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Size-dependent and -independent prey selection of dinoflagellates

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Abstract
Mechanistic approaches to plankton food-webs often rely on size-based models. These models describe predator–prey relationships based on predator body or cell size. However, size-based representations of trophic relationships fail to encompass the diverse feeding behavior of dinoflagellates, which play an essential role in the food-web due to their abundance and ubiquity. Here, we introduce the specialization factor (s) as an effective trait, which aggregates over aspects of morphology, trophic strategy, and feeding behavior and quantifies the degree of specialization towards a specific prey size. We found that specialization to either the upper or lower edge of the prey size spectrum is connected to size independent trophic relations. As a result, dinoflagellates can be divided into three groups with distinct dependencies of optimal prey size on predator size: (1) mixotrophic engulfers specialized on small prey ($s = -1$), (2) pallium feeders on large prey ($s = 1$), and (3) neutral feeders ($s = 0$) encompassing generalist engulfers and tube feeders. Our trait based approach elucidates the evolutionary significance of diverse feeding modes and specialization in dinoflagellates compared to phylogenetically older groups such as ciliates. It furthermore leads to a more accurate representation of trophic relationships of dinoflagellates in models and can provide, more generally, an efficient description of complex and diverse feeding relations in plankton food-webs.

Introduction

Mechanistic studies of aquatic food-webs require an understanding of how plankton groups work as primary producers and consumers (Savage et al. 2007; Wallenstein and Hall 2012; Taherzadeh et al. 2019). The related functions are often formulated based on cell or body size as the main determinant of ecophysiology (Finkel et al. 2010; Serra-Pompei et al. 2020), of the trophic role of an organism in the ecosystem (Barnes et al. 2010; Boyce et al. 2015), or of both (Wirtz and Sommer 2013). In ecological models, trophic relationships are increasingly described by size-based frameworks, thus using predator and prey sizes (Heneghan et al. 2020; Serra-Pompei et al. 2020; Chenillat et al. 2021), which are generally linked via the optimal prey size (OPS) (Fuchs

and Franks 2010; Banas 2011). Being a trait of the predator, the OPS defines who eats whom in the food-web in terms of predator and prey size (Wirtz 2012; Zhang et al. 2014).

The OPS is often assumed to follow a linear function of the predator body size (Hansen et al. 1994; Brose et al. 2006; Jennings et al. 2012). This log-log linear scaling relation has been expanded to include other variables originating from mechanistic considerations such as the feeding mode, which discriminates between filter (passive) and raptorial (active) feeding (Caparroy et al. 2000; Kiørboe 2011). The feeding mode is in turn determined by taxonomic classification (Fuchs and Franks 2010): phylogenetically close organisms share physiological constraints (Kiørboe 2011; Andersen et al. 2016), thus follow similar OPS scaling, characterized by a constant OPS-to-predator size ratio (Hansen et al. 1994; Fuchs and Franks 2010; Kiørboe 2011). The deviation of the OPS-to-predator-size ratio from a neutral value derived for all plankton groups has been defined as feeding mode (see Table 1). The feeding mode seemed to be a constant value for a specific taxa, since phylogenetically close members share the same selectivity constraints (Hansen et al. 1994; Kiørboe 2016). However, for plankton groups with more

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Table 1 Definitions of terms used in this study

Term	Symbol	Definition
Trophic strategy		The way to acquire carbon and nutrients for supporting life. In dinoflagellates, the t. s. forms a continuum from photo(auto)trophy to hetero(phago)trophy (Andersen et al. 2015).
Feeding mechanism		Realization of food acquisition, thus how to find, capture, handle, and digest prey (Kiørboe 2011). The feeding mechanism is in part quantitatively described by the feeding mode (see below). For dinoflagellates, the feeding mechanism comprises direct engulfment, tube feeding, and pallium feeding (Fig. 1) (Verity 1990; Schnepf and Elbrächter 1992).
Predator body size	D	Equivalent spherical diameter (ESD) of the predator. The mean body size of predatory dinoflagellates is $\bar{D} = 26.2\ \mu m$.
Optimal prey size	OPS	Prey size that allows maximal processing (i.e. ingestion and growth) rates of the predator (Hansen et al. 1994; Wirtz 2012).
Feeding mode	m	The deviation of the predator-to-prey ratio from a reference value obtained for all plankton groups (−1.83) (Wirtz 2012). m is associated with the activity during grazing, including prey detection, capture, handling, ingestion, and digestion. Feeding mode values are related to particular feeding mechanisms: $m < 0$ describes passive suspension feeding, while $m \approx 1 - 2$ active ambushing. The mean feeding mode of all dinoflagellates is $\bar{m} = 1.5$ (appendix B.1).
OPS scaling exponent	α	Exponent of the log-log size dependency of OPS on predator body size (OPS $\sim D^{\alpha}$).
OPS scaling offset	m'	Parallel to the feeding mode, quantifies how the predator-to-prey size ratio deviates from the allometric optimal prey-size scaling.
Specialization factor	s	Degree of specialization over a prey size-class. $s = 0$ represents non-specialized predators, which exhibit a linear size allometry for OPS, whereas at $|s| \gg 0$ the predator group/species is highly specialized at a constant OPS. If s is positive, the OPS of the specialized predator is larger than the OPS of a non-specialist, while it is smaller for a negative s.

In boldface, terms introduced herein

complex feeding mechanism a variable feeding mode was found (Wirtz 2012).

Among plankton, dinoflagellates make an ubiquitous group, being adapted to freshwater and marine environments, to pelagic and benthic habitats, with free-living, parasitic, and endosymbiotic habits (Hackett et al. 2004; Gómez 2012). In line with the wide range of habitats and trophic strategies, mixotrophic and heterotrophic dinoflagellates ingest a highly diverse prey spectrum, e.g. from bacteria to metazoans. This spectrum is yet believed to be limited at the species level by a specific trophic strategy, feeding mechanism, and prey taxonomy (e.g. Naustvoll 2000; Jeong et al. 2010; Hansen 2011; Jeong et al. 2016a; Jang et al. 2017). Previous studies on OPS of dinoflagellates suggest a roughly 1:1 OPS-to-predator size ratio, larger than the one observed for other planktonic taxa (Hansen et al. 1994; Fuchs and Franks 2010). However, the underlying dataset only contained 11 observations for heterotrophic species feeding via direct engulfment (Fuchs and Franks 2010) and, therefore, is not representative of the dinoflagellate diversity in feeding behavior and trophic relations. Furthermore, the non-allometric scaling overestimates OPS of mixotrophic dinoflagellates by a factor of 2–3 compared with experimentally observed values. For example, the theoretical OPS of *Akashiwo sanguinea* is 29 μm (García-Oliva et al. 2022) while the observed OPS is 12 μm (*Prorocentrum cordatum = P. minimum*) (Jeong et al. 2010, 2021). The high trait diversity in dinoflagellates with respect to morphology,

trophic strategy, feeding mechanism, and prey taxonomy can be expected to complicate trophic size relationships, which becomes apparent through the dissimilar prey selection of similar sized dinoflagellates of the genus *Takayama* (Jeong et al. 2016a; Lim et al. 2018) and *Alexandrium* (Lee et al. 2016).

Here we review the diversity in trophic size relations found in dinoflagellates and propose a trait-based framework for its efficient description. The new dataset is based on a—to our knowledge—maximal account of available laboratory studies. Its comparison with a new trait-based framework will not only reveal the validity of the latter but should also allow us to mechanistically link the OPS to morphological and behavioral feeding traits as a basis for more general relationships describing the structuring of aquatic food-webs.

Material and methods

Data compilation

We compiled a dataset based on the published literature to explore the relationship between dinoflagellate body size and their minimum, maximum and OPS, trophic strategy, feeding mechanism, and optimal prey taxonomy (Table 1). The dataset ($n = 79$) contains laboratory feeding experiments conducted with dinoflagellates as predator (in the Supplementary Information, SI). Studies were selected based on the
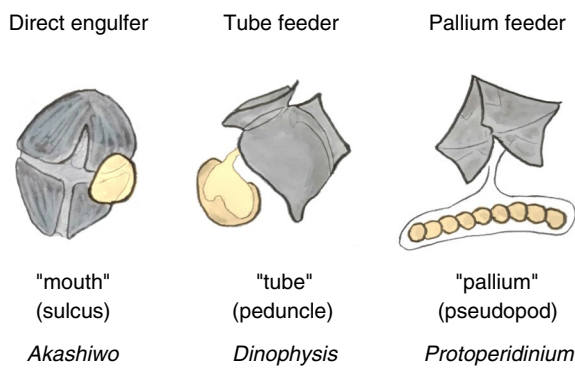
Fig. 1 Schematic representation of feeding mechanisms and structures across different genera of dinoflagellates (prey in yellow). Direct engulfers ingest the entire prey through a body opening; tube feeders suck the cytoplasm from the prey and form an internal digestive vacuole; and pallium feeders externally digest the prey

following criteria: (1) clear taxonomic identification of the predator and prey at least to the genus level for the predator and to the family level for the prey; (2) identification of the feeding mechanism(s); (3) reported predator and prey sizes; (4) controlled and reported light and prey-concentration conditions; and (5) at least the growth, ingestion, or clearance rates should be reported. When OPS was not explicitly specified, we selected the prey (and its size) that maximized the growth rate of the predator. If the growth rate was not available, ingestion—or clearance—rate was used instead. To aid our discussion, additional traits were collected such as cingulum morphology and displacement, sulcus size, presence of 'armour' (theca), swimming speed, colony formation, and photosynthetic ability.

We conducted one way ANCOVA (at a $p < 0.05$ level) to assess statistically significant differences of optimal, maximum, and minimum prey size between trophic strategy and feeding mechanism controlling for the dinoflagellate body size as confounding variable. Trophic strategy is a binary variable: (1) heterotrophic dinoflagellates (HTD), and (2) mixotrophic dinoflagellates (MTD). The feeding mechanism was characterized by three categories: (1) direct engulfment, (2) pallium feeding, and (3) tube feeding. Alternative feeding mechanisms such as tentacle feeding and mucus traps, were not included in the analysis, thus disregarded as exceptional cases. All sizes were expressed as equivalent spherical diameter (ESD) and log-transformed.

OPS scaling and prey specialization

The OPS as function of predator size (OPS scaling) includes size- and non-size-related terms. The latter describe, among others, the activity during grazing, and are aggregated using the feeding mode as a single variable within an extended

scaling theory (Wirtz 2012). This theory separates the effects of size and feeding mechanism by introducing the feeding mode m as a second trait determining OPS independent from predator size D (see Table 1). Here we propose a more general optimal size scaling (OPS $\sim D^\alpha$), or

$$\log(\text{OPS}) = \alpha \log(D) + m',\qquad(1)$$

where α denotes the size scaling exponent for OPS as function of the predator size, and m' an offset independent of predator size. The offset m' is a generalization of the feeding mode, since it encapsulates the size independent aspects of the OPS.

Dinoflagellates form a monophyletic group that follows the archetypal body plan of single-cell heterotrophic organisms (Wisecaver and Hackett 2011; Gómez 2012). This body plan allows the use of direct engulfment as the less evolved and basic feeding mechanism (Jeong et al. 2010). The general OPS scaling thus appears as the typical linear dependence of unicellular plankton which feed via prey engulfment ($\alpha \simeq 1$, Fig. 8 in appendix, Hansen et al. (1994); Fuchs and Franks (2010); Wirtz (2012)). This scaling neglects effects of traits, which do not scale with cell-size: the OPS is assumed to be solely dictated by the size of the predator. However, the realization of more sophisticated feeding behaviors often works independently from the size of the predator. For example, pallium feeders extrudes part of its protoplasm to externally digest their prey (Hansen 1992; Buskey 1997). The size-related constraints of prey engulfment—i.e the size of the prey limited by the size of the internal food vacuole—thus does not apply to pallium feeders, whose OPS differ from the observed for similar sized direct engulfers (Buskey 1997; Naustvoll 2000). Similar to feeding mechanism also other non-size traits such as trophic strategy or optimal prey taxonomy were suggested to be fundamental for the formation of groups within dinoflagellates (Verity 1990; Jeong et al. 2010).

We represent the general OPS scaling of the archetypal dinoflagellates by using the average feeding mode ($\bar{m} = 1.5$, appendix B.1) in a linear OPS scaling ($\alpha = 1$). Deviations on the OPS scaling in terms of variations in m and α then characterize a specific group of dinoflagellates.

These two deviations are here merged into a single variable, which we call the specialization factor s

$$s = m' - \bar{m} - (1 - \alpha)\log(\bar{D}).\qquad(2)$$

The specialization factor s sums over the differences of the scaling exponent α and of the feeding mode m' from their respective overall group averages—(see appendix B for further details)

For a linear OPS scaling ($\alpha = 1$), $s = 0$ if m' is identical to the group averaged feeding mode $\bar{m}$, while $s = -1$ for OPS being a factor e smaller than the group average and $s = 1$

for preferred prey being e-times larger. Hence, the numeric trait s describes deviations from the group average in both directions of the prey spectrum, to smaller and larger prey, and reflects the realized OPS insofar being independent of both group characteristics and predator body size. The specialization factor thus describes the OPS scaling of a group of dinoflagellates with a common feeding behavior. It is here assumed to be closely linked to the degree of specialization of a predator. For example, predation on very large prey such as by pallium feeding is a sophisticated process that is partly decoupled from basic physiological functions of the phagotrophic organism. This process can thus continue in smaller or larger (similarly shaped) organisms. The specialization factor s not only quantifies an offset in the selected prey size spectrum, but is here also interpreted as the strength of prey specialization: size dependency in OPS as given by the exponent α should vanish for increasing deviation, thus increasing absolute value of s. In appendix C we derive a non-linear relationship between this factor and the OPS scaling exponent α

$$\alpha(s) = e^{-as^2}, \tag{3}$$

where the positive constant a quantifies the strength of the link between size-dependence and prey specialization. Low values of a describe a linear OPS scaling with exponent close to one ($\alpha \simeq 1$) even if the OPS shifts to smaller ($s < 0$) or larger ($s > 0$) prey. On the contrary, high values of a increase the dependence of the size scaling exponent on s, so that α vanishes ($\alpha \simeq 0$) at small variations of s, thus much reducing the correlation of OPS with predator size. Our value of a ($a = 4$) is fitted using data for dinoflagellates.

The Eq. 3 links the degree of prey specialization to predatory behavior. Generalist predators that follow the non-allometric scaling are described by $s = 0$ and $\alpha = 1$. On the contrary, predators specialized in large or small prey, $s \gg 0$ or $s \ll 0$, respectively, loose size dependency in OPS ($\alpha = 0$). Intermediate values of s describe moderate degrees of prey specialization such that OPS depends on the predator body size with an exponent $0 < \alpha < 1$.

Model parameter fit

Dinoflagellate species were classified according to their trophic strategy (M = mixotrophic and H = heterotrophic), feeding mechanisms (TF = tube feeding, DE = direct engulfment, and PF = pallium feeding), and optimal prey taxonomy (Cry = cryptophyta, CfD = chain-forming diatoms, Otr = other taxa but cryptophyta and chain-forming diatoms). For each group in this classification, we estimated the OPS scaling exponent α and offset m' via log-log linear regression of OPS and body size (Eq. 1). The specialization factor s was calculated using Eq. 2.

To asses the predictive value of our theory using prey specialization (Eq. 1), we calculated the root-mean-square deviation (RMSD) of predicted vs. observed OPS—in both absolute and logarithmic value—and compared with the RMSD using non-allometric scaling without prey specialization as a reference model: $\alpha = 1$ and $m' = -0.14$, as used in García-Oliva et al. (2022).

Results

Our analysis revealed similarities and dissimilarities of body, optimal, maximum, and minimum prey sizes of dinoflagellates as a function of trophic strategy (Fig. 6 in appendix). The body-size distributions of HTD and MTD are similar since they lack significant differences (ANCOVA, $p > 0.05$). Also, optimal and minimum prey size are similarly distributed among trophic strategies (all ANCOVA, $p > 0.05$). However, maximum prey sizes of HTD are significantly larger with median 31 μm than the ones for MTD with median 12 μm (ANCOVA, $F(1, 18) = 19.7$, $p < 0.001$).

The body-sizes of dinoflagellates vary depending on feeding mechanisms with medians of 14, 22, and 36 μm for tube feeders (TF), direct engulfers (DE), and pallium feeders (PF), respectively (ANCOVA, $F(2, 69) = 4.9$, $p < 0.01$; Fig. 7 in appendix). Similarly, maximum prey sizes significantly differ between feeding mechanisms with medians of 12 (TF), 12 (DE), and 200 μm (PF) (ANCOVA, $F(2, 20) = 7.28$, $p < 0.01$). ANCOVA analyses did not detect any other significant difference in minimum prey size, and OPS across feeding mechanisms (all ANCOVA, $p > 0.05$).

The log-log linear regression of OPS and body size for the whole dataset reveals an allometric scaling, however with considerable scatter (Fig. 2a). This scatter is to a large degree due to heterotrophic pallium feeders grazing over diatoms and mixotrophic direct engulfers grazing over cryptophyta, for which body size ranges cover nearly one order of magnitude while OPS accumulates around 30 and 5 μm ESD, respectively.

OPS for specific feeding mechanisms follows a log-log linear function ($p < 0.05$ for all groups; Table 2). For individual groups, the scatter and related RMSD decrease compared tot he overall scaling for all dinoflagellates. TF and DE prefering dinoflagellates or diatoms as prey exhibit a linear OPS scaling ($\alpha = 1$) (Fig. 2b, c). Yet when the optimal prey is a cryptophyte, OPS becomes independent from predator body size ($\alpha = 0$), thus diverges from the isometric scaling (solid squares in Fig. 2c). This anomaly is observed in MTD but not in HTD. Pallium feeders prefer to feed on chain-forming diatoms in a narrow size range (35–40 μm ESD), whereas predator body size ranges from 20 to 100 μm (solid diamonds in Fig. 2d).
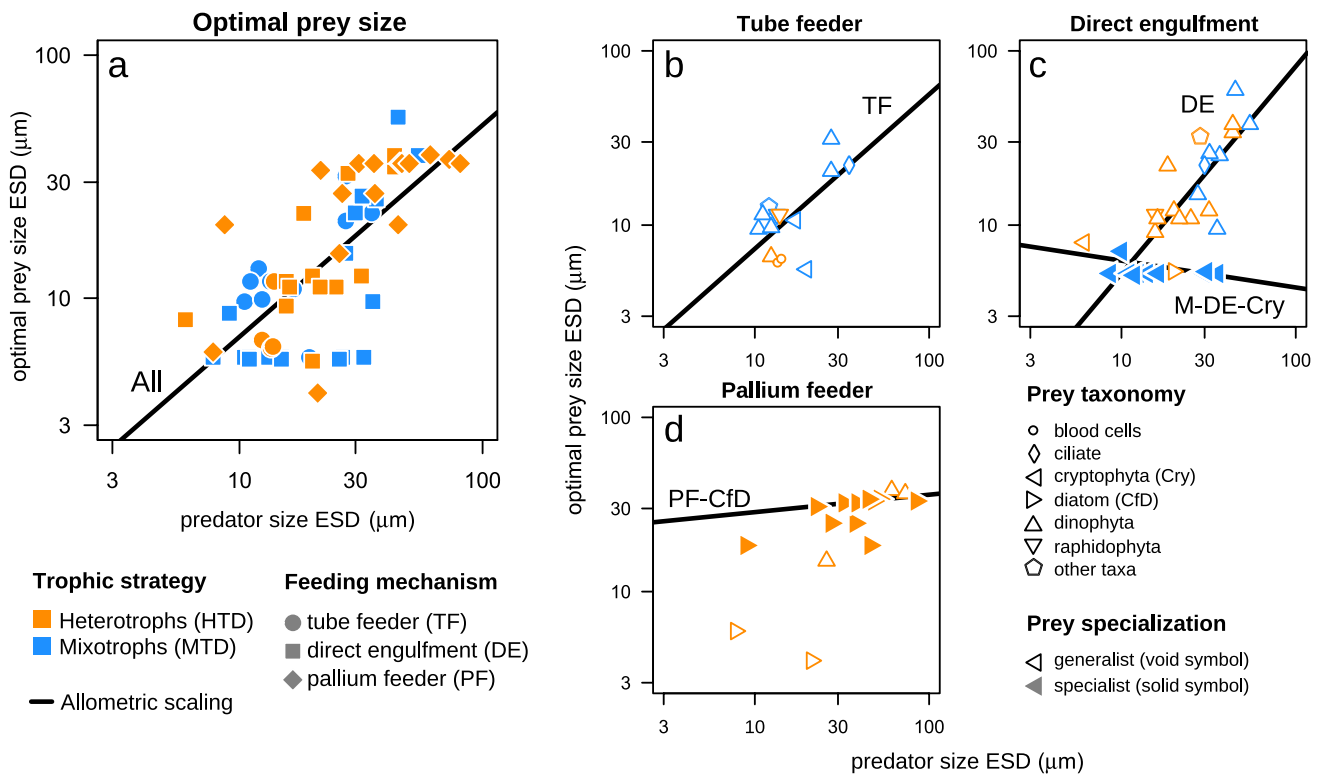
Fig. 2 Optimal prey size (OPS) of as function of predator size. **a** OPS over predator size for dinoflagellates distinguished according to their feeding mechanism and trophic strategy. OPS scaling for dinoflagellates separated with respect to prey taxonomy and feeding mecha-nism: **b** tube feeders, **c** direct engulfers, and **d** pallium feeders. Data points of specialized predators are marked as filled symbols. Values of the fitting lines are given in Table 2. For data sources see SI

The use of prey specialization better reproduces the OPS of dinoflagellates compared with the non-allometric scaling without prey specialization (Fig. 3). The RMSD

Table 2 Scaling exponents α, offset m', and specialization factor s for dinoflagellate groups distinguished according to feeding mechanism, and combinations of feeding mechanism, trophic strategy, and optimal prey taxonomy

Group†	$\alpha \pm \sigma_\alpha$	$m' \pm \sigma_{m'}$	$s \pm \sigma_s$	r^2	n
All	$0.9 \pm 0.1^{***}$	-0.1 ± 0.4	-0.0 ± 0.1	.51	61
TF	$0.9 \pm 0.3^{*}$	-0.0 ± 0.8	0.1 ± 0.2	.40	14
DE	$1.2 \pm 0.3^{***}$	-1.1 ± 0.9	0.0 ± 0.2	.53	19
PF	$0.3 \pm 0.1^{*}$	$2.3 \pm 0.4^{***}$	0.6 ± 0.1	.32	14
H-DE	$0.8 \pm 0.3^{*}$	0.3 ± 0.8	0.3 ± 0.2	.43	13
M-DE	$1.0 \pm 0.2^{***}$	-0.6 ± 0.1	-0.2 ± 0.1	.52	18
M-DE-Cry	-0.1 ± 0.1	$2.0 \pm 0.2^{***}$	-1.0 ± 0.1	.12	11
M-DE-Otr	1.6 ± 0.9	-2.5 ± 3.1	-0.2 ± 0.6	.40	7
PF-CfD	$0.1 \pm 0.1^{*}$	$3.3 \pm 0.1^{***}$	0.8 ± 0.1	.48	11

σ standard deviation, r^2 Pearson's correlation coefficient, n number of observations. Allometries used in the Fig. 2 are in boldface. †Group labels: All = all dinoflagellates, H = heterotrophs, M = mixotrophs, TF = tube feeding, DE = direct engulfment, Cry = feed on crypto-phyta, CfD = feed on chain forming diatoms, Otr = feed on other taxa. Levels of significance: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, no symbol $p > 0.05$

in logarithmic OPS increases from 0.044 for the reference model considering specialization to 0.065 for the variant neglecting specialization model, which means an overall improvement of 26% in terms of log-log RMSD and 28% based on absolute values of OPS. The model improvement differs across dinoflagellate groups. For mixotrophic DE specialized in small prey ($s = -1$) the RMSD without specialization (0.14 for log-OPS, 2.59 for absolute OPS) much exceeds the RMSD of the reference model (0.03 for log-OPS and 0.24 for absolute OPS), with improvements of 76 and 91% for OPS and log-OPS, respectively. For generalist engulfers and tube feeders ($s \simeq 0$), the RMSD of the reference model (0.07 for log-OPS, 1.9 for absolute OPS) only slightly decreased compared to the RMSD of the variant without specialization (0.09 and 2.33, with improvements of 17 and 18%, respectively). For heterotrophic PF ($s = 1$), the RMSD without specialization (0.15 for log-OPS, 3.17 for absolute OPS) much exceeds the RMSD of the reference model (0.01 for log-OPS and 0.32 for absolute OPS), which is analog to an error reduction of 94% and 91% for OPS and log-OPS, respectively. Again, RMSD of the reference model (0.05 and 1.35) is much smaller than for the simpler model version (0.14 and 2.79). Most importantly, the integration of

Fig. 3 Comparison of observed and calculated OPS for dinoflagellates using the non-allometric scaling without (left, $s = 0$) and with prey specialization (right). (RMSD = root mean square deviation.)
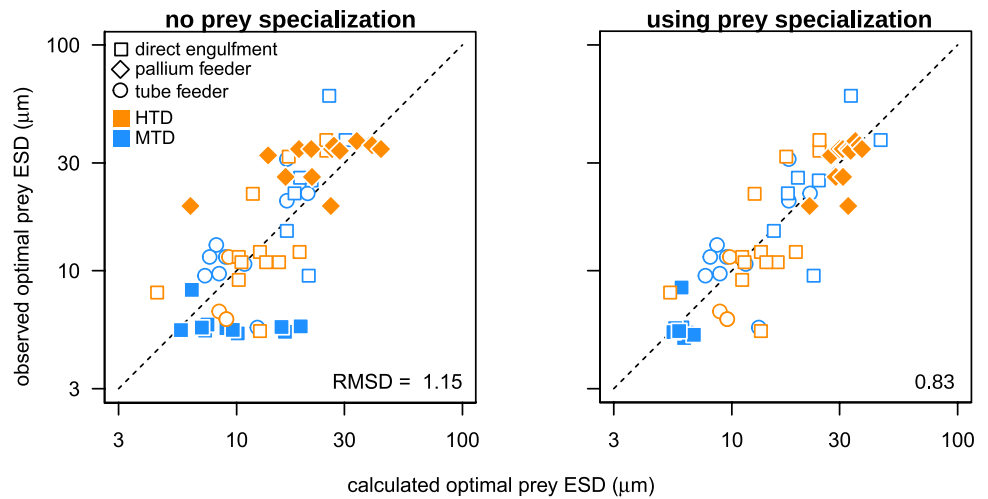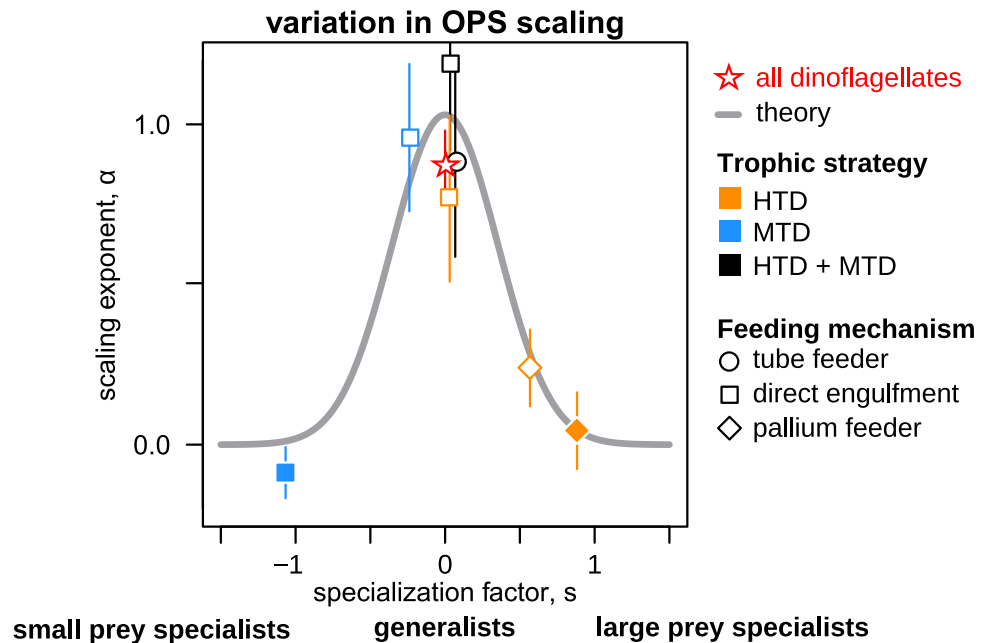

Fig. 4 Scaling exponent α as function of the specialization factor s for diverse groups, both for specialists (solid symbols) and non-specialists (open symbols). For comparison, the theoretical relation used in our trait-based model is shown as a gray line $\alpha(s) = e^{-4s^2}$

prey specialization in the OPS scaling reduces the dispersion of predicted values around 5 and 30 μm ESD.

The fitted scaling exponent α scatters around $\alpha \simeq 1$ for generalists with small s and around $\alpha \simeq 0$ for specialists ($|s| > 0.5$) and, thus, closely matches the theoretically proposed Gaussian relationship with the specialization factor s (Fig. 4).

Discussion

The combined use of body-size D and specialization factor s improves the representation of the OPS of dinoflagellates compared to a description based only on size (Fig. 3). This improvement is especially significant when feeding behavior and prey taxonomy gain importance. These predator traits were aggregated and made effective in the OPS scaling by the use of the specialization factor as a unique trait.

Dinoflagellates feeding groups

Contrary to the assumption of dinoflagellates as a single predator group that follows a unique OPS scaling (Fuchs and Franks 2010; Wirtz 2012), our study identifies three feeding groups by their specialization factor: (1) MTD direct engulfers specialized on small prey ($s = -1$), (2) HTD pallium feeders specialized on large prey ($s = 1$), and

a generalist group of (3) neutral feeders ($s = 0$), encompassing generalist engulfers and tube feeders.

MTD direct engulfers specialized on small prey

MTD that prefer to feed on cryptophyta have a nearly constant OPS of approximately 5 μm, with the lowest specialization factor among all groups of dinoflagellates ($s = -1$). It has been thought that direct engulfment is the less evolved of feeding mechanisms in dinoflagellates (Jeong et al. 2010), as being restricted to a small size range of suitable prey, here quantified by the maximum prey size.

The preference of MTD over cryptophyta suggests an ancestral trait, which recall the endosymbiotic origin of the chloroplasts of dinoflagellates (Raven et al. 2009; Stoecker et al. 2009; Park et al. 2013, 2014). Most orders of dinoflagellates such as Gonyaulacales, Gymnodiniales, Peridiniales, and Prorocentrales have members with peridinin-containing plastids derived from red algae, which are also present in cryptophyta (Bodył and Moszczyński 2006; Zapata et al. 2012). Phagotrophy through direct engulfment may have originally been used by MTD to acquire photosynthetic machinery from their prey by endosymbionts or kleptoplastids, depending on the degree of reduction of the retained material (Park et al. 2014; Mitra et al. 2016). This group may include endosymbiotic specialists non-constitutive mixotrophs, which retain the photosynthetic functions of the ingested prey to aquire phototrophy (Mitra et al. 2016). This trait can be expressed under limitation of photosynthetic conditions (Jeong et al. 2005b). The deviations of the OPS from the general-linear size scaling of this group as well as the specialization over a specific prey type would then follow from a derived but ancestral behavior, which remained unaltered after size diversification.

HTD pallium feeders specialized on large prey

Pallium feeders (PF) are thecate HTD, with less diverse optimal prey taxonomy and larger prey size than direct engulfers and tube feeders. This group is here described by a high specialization factor ($s = 1$). Even though PF are well differentiated from the other dinoflagellates groups, they still share the same size-scaling that apply to dinoflagellates as a whole in form of growth rate, carbon and nitrogen content (Menden-Deuer and Lessard 2000; Menden-Deuer et al. 2005). However, the OPS scaling of this group deviates from the general trend of all dinoflagellates. PF grow faster when fed on diatoms, systematically selecting diatoms over dinoflagellates presumably influenced by chemosensory signals and not prey size (Buskey 1997; Naustvoll 2000). Prey

motility may play an important role for the preference of (non-motile) diatoms over (motile) dinoflagellates (Buskey 1997; Naustvoll 2000).

The size of the suitable prey of PF is limited by the amount of pseudopodium available for pallium formation, which sets an upper limit beyond which the capture becomes inefficient (Naustvoll 1998, 2000). This limit has been observed far larger than the dinoflagellate cell size, in some cases up to prey with tenfold larger diameters than the one of the predator (v.g. Jacobson and Anderson 1986; Jacobson 1987; Strom and Buskey 1993). However, the effectiveness of digestion may decrease with larger prey due to gut based transport (Wirtz 2014), constraining the practical maximum prey size to approximately four times the predator body diameter. For example, *Protoperidinium pallidum* and *Zygabikodinium lenticulatum*, with body sizes of about 50 μm ESD feed on items with ESD of about 200 μm (Naustvoll 2000). Pallium formation allows an external digestion of the prey, so that the prey size decouples from predator size. This disengagement explains of (1) a larger maximum prey size of PF compared with TF and DE, and (2) size independent prey selection of PF ($\alpha \simeq 0$).

Neutral feeders

Generalist direct engulfers feeding on dinoflagellates, ciliates and other taxa, and tube feeders were here grouped to neutral feeders. The DE in this groups have no preferred optimal prey taxonomy and hence are termed 'generalist engulfers'. This group follows the general OPS scaling with a neutral specialization factor ($s = 0$), and can thus be regarded as an archetypal group.

Despite of the size-independence of tube feeding (Verity 1990; Berge et al. 2008), TF follow a linear size scaling, similar to the strongly size-constrained DE. For instance, the prey size range of tube feeding *Karlodinium armiger* spans from 5 to 31 μm, with an OPS around 13 μm (Berge et al. 2008), which is nearly identical to similar sized DE (Hansen et al. 1994; Hansen and Calado 1999). TF make the least diverse group in terms of size, but contain prominent and ecological relevant members such as the genus *Dinophysis* (Park et al. 2008).

Some exclusive predator–prey relationships are fixed by physiological limitations of tube feeding dinoflagellates. For example, the kleptoplastic obligate phototrophs *Dinophysis* spp. use plastids of cryptophyte origin, acquired only by depredation on the ciliate *Mesodinium rubrum* (= *Myrionecta rubra*) (Park et al. 2008, 2014). This specialization creates an exclusive trophic interaction between these dinoflagellates and its ciliate prey. A similar behavior has been observed for *Durinskia* spp. feeding on diatoms (Yamada

et al. 2019) as for other genera (Jang et al. 2017; Jeong et al. 2021). These OPS relationships partially reflect the size-dependence of encounter rates (Kiørboe 2011), but are mostly determined by other physiological traits, specifically of those of plastidic specialist non-constitutive mixotrophs (Mitra et al. 2016).

Neutral feeders comprising both MTD and HTD can feed on other dinoflagellates. This ability of intra guild predation (Prowe et al. 2022) might be of high eco-evolutionary significance, since it is closely related to bloom formation and dinoflagellates dominance (Jeong et al. 2021; García-Oliva et al. 2022).

One species but multiple feeding mechanisms

The expression of more than one feeding mechanism is possible within a single dinoflagellate species (Jeong et al. 2010). An often observed combination is direct engulfment of small prey and tube feeding such as by *Karlodinium* spp., *Gyrodinium instriatum*, and *Takayama helix* (Uchida et al. 1997; Jeong et al. 2016b; Yang et al. 2021) ($s = -1$–0). In these cases, the utilized feeding mechanism depends on the

prey size: small prey is directly engulfed (with an effective specialization factor of $s = -1$), while the content of large cells is sucked using a tube ($s = 0$).

The expresion of multiple feeding mechanisms broadens the available prey size-spectrum, and it is suspected to facilitate dominance and maintenance of dinoflagellate blooms (Yang et al. 2021). A diverse prey spectrum has been suggested as an adaptive advantage that helps some species of MTD to be globally dominant (Jeong et al. 2021). As a consequence, the specialization factor of dinoflagellates might be an adaptive trait, suspected to depend on prey availability and the adaptability of the dinoflagellates community. The expression of multiple feeding strategies through a variable feeding mode may be in particular important for understanding the dynamics of aquatic food-webs.

Origin of the specialization factor

In our theory, the reference body size $\bar{D}$ and feeding mode $\bar{m}$ (the mean body-size and feeding mode of dinoflagellates, respectively) in combination describe the neutral

Fig. 5 Schematic summary of our findings. Predator traits (trophic strategy, feeding mechanism and cell morphology) are related to the specialization factor *s*. The OPS is proportional to the predator body size for $s = 0$. Constant OPS is observed for $s = -1$ and 1. Some remarkable examples are: **a** non-sulcus mixotroph direct engulfer *Prorocentrum micans*, **b** non-overlapping cingulum mixotroph direct engulfer *Gymnodinium* sp., **c** overlapping cingulum direct engulfer *Gyrodinium spirale*, **d** tube feeder *Dinophysis* sp., and **e** pallium feeder *Protoperidinium* sp.
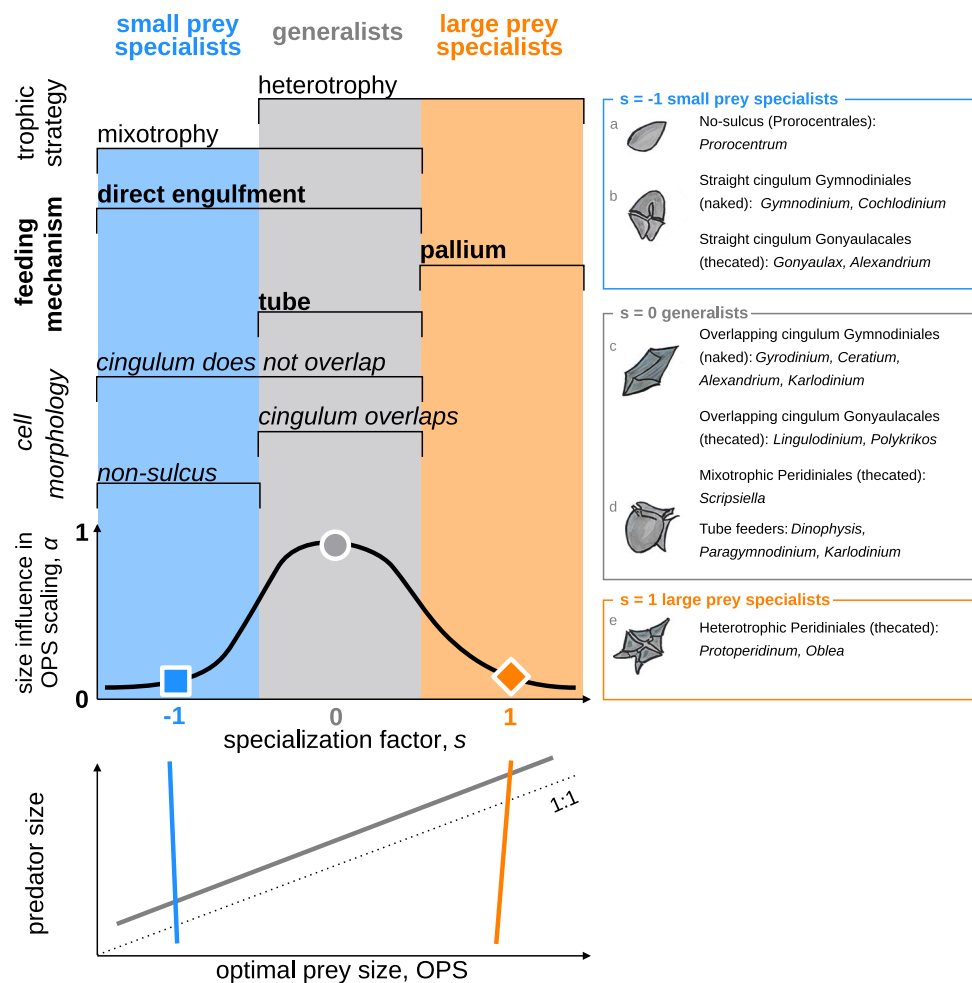
OPS scaling ($\alpha = 1$ and $s = 0$) of dinoflagellates as a whole (the archetypal dinoflagellates), which reinforces the idea of dinoflagellates as a single predator group. All dinoflagellates share structural and bio-physiological size allometries, constraints, and behaviors. However, as the use of the specialization factor helps to differentiate intra-group differences in the ecological role insofar independent of predator size.

The specialization factor was here derived starting from a (size) scaling law of OPS with the aim to capture non-size traits shaping the feeding process. These non-size traits constraint the OPS in any stage of the prey acquisition. For example, the shape and size of the sulcus fix the 'mouth-size' of direct engulfer dinoflagellates limiting the size of the prey that can be acquired (Jeong et al. 2010). Sulcus size is partially determined by cingulum shape: an overlapping cingulum creates a larger and more flexible sulcus than a straight cingulum (Jeong et al. 2010). As a non-size trait, cingulum shape follows a phylogenetic classification, in which we observe two distincts effects on the specialization factor: (1) Within the order Gymnodiniales (Reñé et al. 2015), cingulum shape and specialization factor are related at the genus level: straight-cingulum *Gymnodinium* spp. are specialized on small prey ($s = -1$), while *Gyrodinium* spp. with their overlapping-cingulum are generalized engulfers ($s = 0$). (2) The order Prorocentrales lack a sulcus due to their thecal configuration. Their prey is thus ingested through the inter-plate sutures, limiting the size of ingestable prey (Jeong et al. 2005b). *Prorocentrum* spp. are hence specialists on small prey ($s = -1$).

Alike for cingulum shape, other traits might be involved in the determination of the specialization factor such as photosynthetic abilities, armour, swimming speed, chain formation, prey motility, or prey handling time. However, the complexity of feeding mechanisms in dinoflagellates challenges the identification of clear-cut effects of these traits on prey selection. The consideration of non-size traits may guide future research, both for dinoflagellates and other plankton groups. We present a schematic summary of our findings in Fig. 5. A further discussion on this topic is given in appendix D.

Ecological significance of specialization beyond dinoflagellates

Our results sustain the idea that OPS of dinoflagellates follows a general body-size scaling, in agreement with theories that apply to planktonic predators in general (Boyce et al. 2015; Andersen et al. 2016). These theories assume a constant OPS to predator body size ratio for a predator group. While this assumption holds for simple taxa such as ciliates and flagellates (Hansen et al. 1994; Fuchs and Franks 2010), or for groups classified by feeding mechanism such as active and passive grazing (Kiørboe 2011; Wirtz 2012; Kiørboe et al. 2018), some exceptional but important groups deviate from this assumption such as pelagic tunicates, thecosome pteropods (Conley et al. 2018), salps (Stukel et al. 2021), jellyfish, copepods (Wirtz 2012), chaetognaths (Pearre 1980), and dinoflagellates (Jeong et al. 2010). All these groups express some degree of prey specialization ($\alpha \simeq 0$). Prey specialization is thus a common trait spread along the entire aquatic food-web.

Through this study of dinoflagellate OPS scaling, we hypothesize two common traits in groups that express prey specialization: (1) high morphological diversity, and (2) complex predatory behavior. In consequence, simpler, less-diverse, and phylogenetically older taxa such as ciliates and flagellates, show smaller deviations from a linear OPS scaling, compared with those of more complex and diverse taxa such as dinoflagellates, copepods, and jellyfish (Wirtz 2012). These ideas are yet to be tested and might motivate further research.

Conclusion

The biomechanical constraints imposed by trophic strategy—heterotrophy or mixotrophy–, feeding mechanism –direct engulfers, tube, or pallium feeder–and prey selection, quantified altogether by the specialization factor, play a major role in the OPS scaling of dinoflagellates. We identify three dinoflagellates feeding groups by their specialization factor. Two of these groups are highly specialized in a prey type and reveal a small size dependence: (1) mixotrophic engulfers feeding on small prey ($s = -1$), and (2) pallium feeders on large prey ($s = 1$)–; a third group comprises generalist engulfers and tube feeders with a strong body-size dependency ($s = 0$). The combined use of body-size and specialization factor points to the evolutionary significance of diverse feeding behaviors and specialization in dinoflagellates compared with older groups as ciliates. We propose that the range in specialization factors found for dinoflagellates efficiently describes their diversity of feeding mechanisms.

Appendix A: Additional figures

Fig. 6 Body, optimal, maximum, and minimum prey sizes by trophic strategy of dinoflagellates. The median size shown as an horizontal line. Vertical lines and boxes are over the 5–95 and 25–75 percentiles, respectively. The number of observations are over each symbol. *Only maximum prey size show significant differences regarding trophic strategy ($p < .001$). Data after diverse sources (see SI for the entire list of references)
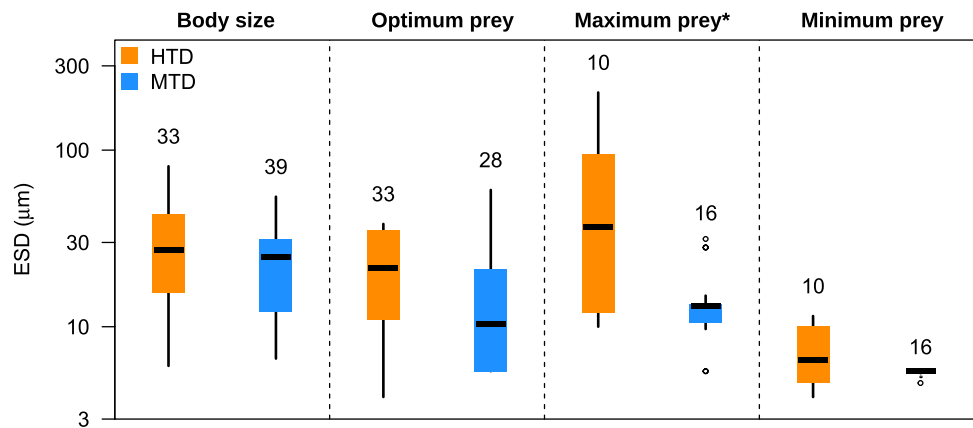
Fig. 7 Body, optimal, maximum, and minimum prey sizes by feeding mechanism of dinoflagellates. The median size shown as an horizontal line. Vertical lines and boxes are over the 5–95 and 25–75 percentiles, respectively. The number of observations are over each symbol. *Body and maximum prey size show significant differences regarding feeding mechanism ($p < .01$). Data after diverse sources (see SI for the entire list of references)
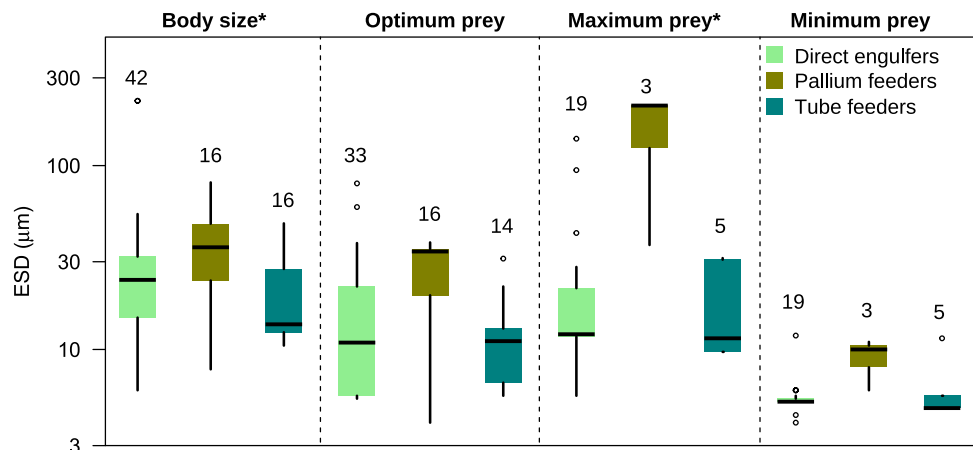
Appendix B: The general OPS scaling of archetypal dinoflagellates

Dinoflagellates follow the simple body plan of unicellular heterotrophic plankton such as ciliates and flagellates. However, dinoflagellates express additional traits—i.e. two flagella, pusule, high DNA content, etc.—, which separate dinoflagellates from other taxa. Dinoflagellates in turn form a highly diversified taxa, which is comprised by groups that express specific traits—e.g. armour (theca), morphology, feeding mechanism, living habits, etc. These specific traits can be independent of size and potentially modify the body plan of the dinoflagellates. We here propose a group of generic dinoflagellates, which follows the simplest body plan of unicellular plankton with no non-size traits: size alone is thus the master trait that describe all the ecological functions of this group. This group as a mere idealization does not represent any particular dinoflagellate, but intend to represent dinoflagellates as a whole. Our proposed idealization is regarded as the group of archetypal dinoflagellates.

The group of archetypal dinoflagellates is assumed to follow the simplest OPS scaling law ($\alpha \simeq 1$, Fig. 8), the one of those unicellular plankton. This scaling law can be described by the non-allometric scaling (Wirtz 2012)

$$\log(\text{OPS}) = \log(D) + m, \tag{B1}$$

where D is the predator size, and m is the feeding mode. The feeding mode is a proxy for the OPS to predator size ratio

$$\frac{\text{OPS}}{D} = e^m. \tag{B2}$$

This formulation is based on two hypothesis: (1) the OPS is linearly correlated to the body size (OPS $\propto D$), and (2) the OPS to predator size ratio is constant and independent of the body-size (m is a constant). The feeding mode is associated with the activity during grazing, including prey detection, capture, handling, ingestion, and digestion (Wirtz 2012). We propose that any deviation of the grazing-related activities relative to the general behavior may affect the OPS to
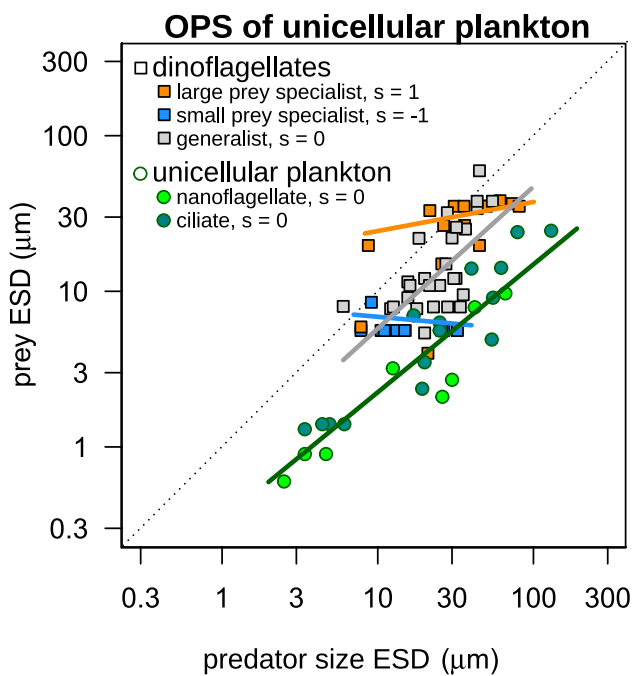
Fig. 8 OPS scaling of unicellular plankton: dinoflagellates, ciliates and nanoflagellates. OPS calculated using the spezialization factor (lines). Data from (Fuchs and Franks 2010)

predator size ratio, which follows a power-law dependence on predator size

$$e^m \propto D^\beta, \tag{B3}$$

where β is an arbitrary constant that combines the scaling laws of all traits related to the feeding activities. This scaling law is compared to the reference values for size $\bar{D}$ and feeding mode $\bar{m}$ as

$$\frac{e^m}{e^{\bar{m}}} \propto \left[\frac{D}{\bar{D}}\right]^\beta. \tag{B4}$$

These ratios represent the deviation of a dinoflagellate from the archetypal group in the OPS scaling, which is represented by a linear scaling exponent with a constant feeding mode. The dependence of non-size traits is here represented by β. The OPS-to-body size ratio is then

$$m - \bar{m} \propto \beta \left[\log(D) - \log(\bar{D})\right], \tag{B5}$$

expression from which after the addition of a constant s to create an equation, we obtain

$$m - \bar{m} = \beta \log(D/\bar{D}) + s. \tag{B6}$$

We interpret s as the 'specialization factor', which reflects the degree of specialization over a prey size. This interpretation comes after the comparison of both non-allometric OPS scaling (Eq. B1) and the allometric scaling herein proposed

(Eq. 1). The specialization factor here describes the expression of both size- and non-size-related dependencies of the OPS. This regulation is mediated through variable feeding modes as suggested by Eq. B6.

The introduction of a reference body size in Eq. B6 allows the interpretation of the specialization factor as numerically equal to the feeding mode when the body size equals the reference value.

Matching the equation for the scaling of the feeding mode (Eq. B6) and the allometric prey size-scaling (Eq. B1) yields

$$\alpha = \beta + 1, \text{ and } m' = \bar{m} + s - \beta \log(\bar{D}). \tag{B7}$$

If $\beta = 0$, the scaling exponent and feeding mode respectively are $\alpha = 1$ and $m' = \bar{m} + s$. In this case the allometric scaling (Eq. 1) converges to the non-allometric scaling (Eq. B1) with the sum of the mean feeding mode and the specialization factor replacing the feeding mode, which under linear conditions ($\alpha = 1$), are equivalent

$$\log(\text{OPS}) = \log(D) + \bar{m} + s. \tag{B8}$$

From the Eq. B8, we assume that for $s = 0$, the OPS scaling follows the generic archetypal OPS scaling (Eq. B1). As a consequence, $s = 0$ is reserved for the representation of the most general feeding behavior of dinoflagellates: the one that assumes (1) a linear dependence of the OPS in function of size ($\alpha \simeq 1$), and (2) a constant OPS to body size ratio (in terms of the feeding mode, $e^{\bar{m}}$ is a constant).

B.1 Size scaling of the functional feeding mode *m*

The feeding mode of dinoflagellates spans from 0 to 3. The feeding mode is independent of the relative log-size ($p > 0.05$, $r^2 = 0.01$, $n = 61$), with a constant value of $\bar{m} = 1.51 \pm 0.52$. The feeding mode as function of relative log-size of pallium feeders grazing over diatoms follows a linear trend $m = 3.06 - 0.8 \log(D/\bar{D})$ ($p < 0.001$, $r^2 = .64$, $n = 11$), as well as direct engulfers grazing over cryptophyta $m = 0.49 - 0.98 \log(D/\bar{D})$ ($p < 0.001$, $r^2 = 0.94$, $n = 11$).

Proposing a size-scaling for a feeding mode might involve the individual quantification of the scaling laws for each one of the traits included in the activities of predation (Kiørboe 2011, 2016). The particularities of the predation process must be therefore explicitly taken into account. We simplified this idea under the assumption that the combined effect of all traits is represented by a single scaling factor β, which characterizes the size-scaling of the all the traits involved in the feeding mechanism (Eq. B6). The size-scaling of the feeding mode is expressed as a linear function of the logarithm of a relative body size $\log(D/\bar{D})$, where $\bar{D}$ is a reference body size defined as the mean size of the predators (Eq. B6). The introduction of the reference body size allows to compare the feeding modes of different feeding

groups ignoring the size scaling effects introduced by β at this particular body size. This comparison originates the specialization factor s as a trait. The value of the specialization factor s is then the value of the feeding mode m of a group of predator expressed at the reference body-size.

Appendix C: The scaling exponent α as function of the specialization factor s

We introduce the scaling exponent α and the specialization s as two free parameters in the size scaling of the OPS. However, we can link both variables based on symmetry and optimality arguments. First, Eq. 1 converges to Eq. B1 for $\alpha = 1$, thus $\beta = 0$. Under this conditions, Eq. 1 reads

$$\log(\text{OPS}) = \log(D) + \bar{m} + s. \tag{C1}$$

When $\beta = 0$ the offset is assumed to be equal to a general 'neutral feeding mode' $\bar{m} + s$. Second, the feeding mode m of a group of predators which follows a linear optimal prey scaling ($\alpha = 1$) is numerically equal to the specialization factor s (i.e. $m = s$). In consequence, since Eq. C1 is the non-allometric scaling (Eq. B1), $s = 0$ is the specialization factor of a non-specialized predator, thus defines a 'neutral' behavior.

Highly specialized predators show no size-dependence in the OPS, thus $\alpha = 0$ and in consequence $\beta = -1$ (see Eq. B7). We assume that prey specialization is possible in both extremes: a predator is able to specialize on either larger or smaller prey than the size fixed by the neutral reference value (the one expressed when $s = 0$). The specialization over larger and smaller prey are respectively expressed by s_+ and s_-, which correspond to the values that reproduce a constant OPS. Here s_+ is higher and s_- is lower value than 0. We then propose a functional link between α and s expressed with the notation $\alpha(s)$—read as 'α is function of s'.

Equation 1 can be rewritten

$$\log(\text{OPS}_\pm) = \log(\bar{D}) + \bar{m} + s_\pm, \tag{C2}$$

where D_+ and D_- are the constant OPSs which are respectively larger and smaller than the expected value expressed by the neutral behavior. This last value is calculated from the evaluation of Eq. C1 at the reference body size $\bar{D}$, which yields

$$\log(\text{OPS}_0) = \log(\bar{D}) + \bar{m}. \tag{C3}$$

From the direct comparison of Eqs. C2 and C3, we impose the following relations:

(i) $s_- < 0 < s_+$
(ii) $\text{OPS}_- < \text{OPS}_0 < \text{OPS}_+$
(iii) $\alpha(s_-) < \alpha(0) > \alpha(s_+)$
(iv) $\alpha(s_-) = \alpha(s_+) = 0$, and
(v) $\alpha(0) = 1$.

From these we can infer that $\alpha(s)$ has a maximum at s_0, and is symmetrical around this value. Therefore we propose that α depends on s^2. In first instance, and due the reduced knowledge of our system, we assume a simple Gaussian function

$$\alpha(s) = e^{-as^2} \tag{C4}$$

that fulfill the imposed conditions.

The real functional form of α as function of s might be more complex. However, as indicated by our results such as Fig. 4, this simpler approach yields a reasonable description of the observed optimal-body size relationships for dinoflagellates.

Appendix D: Traits related to the specialization factor

D.1 Trophic strategy and feeding mechanism

Dinoflagellates express diverse trophic strategies, ranging from strict auto(photo)-trophy to strict hetero(phago)-trophy, stepping into mixotrophy (Stoecker 1999; Hansen 2011). About half of the known dinoflagellate species are photosynthetic—potentially mixotrophic (Yoo et al. 2013)–, while the other half are strict heterotrophic (Taylor et al. 2008; Gómez 2012).

Hetero- and mixo- trophic dinoflagellates utilize one of these major feeding mechanisms: direct engulfment (phagocytosis), tube feeding (myzocytosis), or pallium feeding (external digestion) (Verity 1990; Schnepf and Elbrächter 1992; Taylor et al. 2008) (Fig. 1). Direct engulfing occurs when the prey is completely incorporated via a digestive vacuole. This mechanism is used by many naked (Schnepf and Elbrächter 1992; Jacobson and Anderson 1996; Hansen and Calado 1999; Taylor et al. 2008) and thecate (Skovgaard 1996; Jeong et al. 2005a, b, c, 2010) genera. In all these, the prey is entirely engulfed through the middle or posterior part of the sulcus, the apical horn, or the suture (Jeong et al. 2005c, 2010). Tube feeders use peduncles or phagopods—i.e. tubular structures—to ingest the cytoplasm and/or organelles of their prey (Verity 1990; Hansen and Calado 1999). Pallium feeders extrude a portion of their cytoplasm to externally engulf their prey (Gaines and Taylor 1984; Jacobson and Anderson 1986; Jeong et al. 2010). This mechanism is used exclusively by thecate dinoflagellates (Schnepf and Elbrächter 1992). The digestive area of pallium feeders scales proportional to the prey size (Schnepf and Elbrächter 1992; Taylor et al. 2008). Some species use multiple feeding

mechanisms—e.g. some *Karlodinium* spp.–(Uchida et al. 1997; Jeong et al. 2016b; Yang et al. 2021).

D.2 Traits estimated to contribute to the specialization factor

From our dataset, we estimated the effect on specialization of armour presence, swimming speed, colony formation, prey handling time, mixotrophy and photosynthetic abilities, which are involved during the activities of predation of dinoflagellates.

Armour. The presence of thecal plates is a trait related to feeding behavior: pallium feeders ($s = 1$) are always thecate species. However, the presence or absence of thecal plates is not related to direct engulfment nor tube feeding, which contain both, armoured and naked taxa. Thecate species has been observed to engulf small prey through the apical cone suture (Jeong et al. 2005b, 2010).

Predator and prey swimming speed. Apart from its role as regulator of the vertical habitat selection (Smayda 2010; Wirtz and Smith 2020), swimming speed is a key variable in the biomechanics of prey capture (Hansen and Calado 1999; Kiørboe et al. 2018; Lim et al. 2018; Talmy et al. 2019). Swimming speed defines which prey a predators can get when no immobilization mechanisms are utilized such as toxins, nematocysts, mucus traps, etc. (Jang et al. 2017). Swimming capabilities, in combination with cell morphology, allows free-swimming dinoflagellates the

maximum swimming speed

Fig. 9 Maximum swimming speed v as function of dinoflagellate body size. The correlation is not significant $v = 164.6 + 68.5 \, \log(D)$ ($r^2 = .02$, $p = .42$, $n = 19$). Data from Smayda (2010)

use of feeding currents, which facilitate higher encounter rates and aid the prey capture process, specially of small prey ingested through the sulcus or the apical apertures (Fenchel 2001; Nielsen and Kiørboe 2015). Prey availability regulate the swimming pattern and speed of predator dinoflagellates (Strom and Buskey 1993; Buskey 1997), which indicates that prey acquisition encourages active swimming. No significant relationship between maximum swimming speed and cell size has been found for dinoflagellates (Fig. 9) (see also Jeong et al. 2015), and the effects of other traits on maximum swimming speed of dinoflagellates remain unclear (Jeong et al. 2010; Lim et al. 2019). However, the specialization factor seems to be linked with the prey's swimming speed: Pallium feeders ($s = 1$) prefer to feed non-motile diatoms (Buskey 1997). In contrast, generalist engulfers ($s = 0$) and mixotrophic engulfers specialized on small prey ($s = -1$) prefer to feed on prey with similar speed than the predator (Jeong et al. 2016a; Lim et al. 2018).

Chain and colony formation. Chain-formation affects the processes of prey detection and capture: chain-arranged dinoflagellates are faster swimmers than individual cells (Smayda 2010; Sohn et al. 2011). This allows dinoflagellates to chase and effectively capture fast prey, which as individual cells would result in a failure (Smayda 2002). Chain-forming direct engulfers ($s = -1$) feed more frequently on motile prey (Uchida et al. 1997) than single-cell species, which prefer to feed more on non-motile prey ($s = 1$). As for swimming speed, the relationship of colony formation of dinoflagellates with the OPS, trophic strategy, and feeding mechanism are still an unattended topic.

Handling time. Measured either as total feeding time or time for engulfment, handling time appears as an additional predator's trait related to prey selection: the optimal prey is often the one that minimize the handling time. This has been observed for direct engulfers MTD (Jeong et al. 2005b), pallium feeders HTD (Buskey 1997), and, in some degree, in tube feeders (Lim et al. 2018). Handling time and prey size are negatively correlated (Jeong et al. 2005b; Gonçalves et al. 2014), which creates a trade-off condition between the time spent in the feeding process and the energetic profitability of captured prey. This trade-off is related to feeding mechanism, which creates what we identify as two divergent strategies: In the first, small prey specialists ($s = -1$) feed frequently spending low energy and short times per each attained item—e.g. 100 seconds per engulfed item of the optimal prey in the direct engulfer MTD *Lingulodinium polyedrum* (Jeong et al. 2005b)—with the capacity of consuming multiple items simultaneously, but receiving low energy per each consumed prey. In the second, large prey specialists ($s = 1$) feed sparingly spending high energy and long times per attained item—e.g. 13.9 min per captured item of the optimal prey in
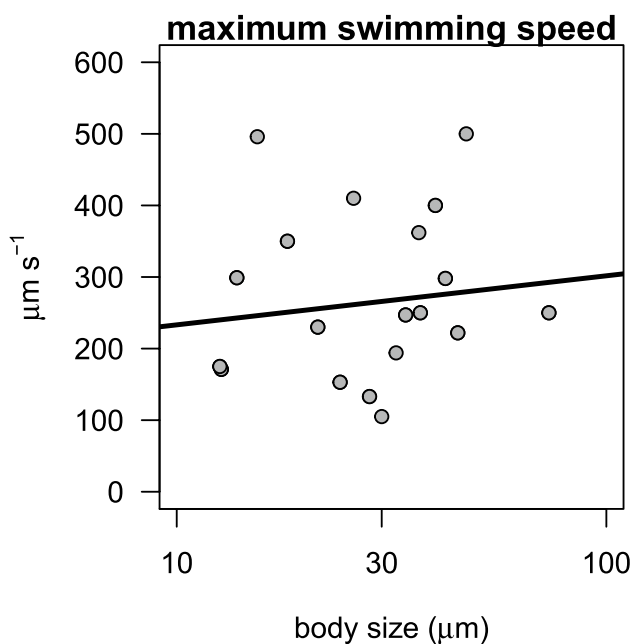
the pallium feeder *Protoperidinium pellucidum* (Buskey 1997)—with the capacity of consuming only a single item by a time, but receiving high energy per each consumed prey. Thus, prey handling time is a trait to optimize during the prey selection process.

Trophic strategy. Mixotrophy does not affect the minimum prey size of dinoflagellates but is connected to smaller optimal and maximum prey sizes. We suggest that the difference in the maximal prey size range derives from pallium feeding ($s = 1$), which is exclusively used by HTD and allows the ingestion of larger prey compared to the one for the other feeding mechanisms.

Origin of the photosynthetic abilities. Closely related to trophic strategy, the origin of photosynthetic abilities on dinoflagellates might play a role in optimal prey selection. Kleptoplastic species—i.e. non-constitutive mixotrophs that acquire photosynthetic abilities by the retention of chloroplast of their prey—tend to select prey that can provide chloroplasts suitable to keep the photosynthetic machinery running (Mitra et al. 2016). This is especially observed in *Dinophysis* spp. and their specificity over the ciliate *Mesodinium rubrum*, which contains kleptoplastids originated of red algae (Park et al. 2008, 2014). The amount of resources assigned to autotrophy in MTD might affect prey selection, as well as might affect the obligatoriness of photosynthesis and phagotrophy for dinoflagellate growth (Hansen and Calado 1999; Stoecker 1999). This relates the energetic demands of dinoflagellates with the energy demanded for the predatory activities. The relationship of photosynthetic activity and OPS has not been studied in direct engulfers. The consideration of the here discussed and other traits –in which their influence on predation are not yet clear—may guide future research regarding the feeding behavior of dinoflagellates.

Declarations

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