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# LIMNOLOGY and OCEANOGRAPHY



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# Short handling times allow for active prey selection in suspension feeding copepods

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#### Abstract

The time it takes copepods to handle prey can vary depending on the properties of the prey, but it is still largely unknown how handling times may affect copepod feeding efficiency. We compiled data on preyhandling times derived from video observations in 10 species of calanoid and cyclopoid copepods consuming a large variety of prey. Prey-handling times vary by five orders of magnitude, and the largest fraction of this variation is explained by relative prey size: larger prey takes longer to handle. When normalized by prey volume (volume of prey handled per unit time), however, larger prey are handled more efficiently than smaller prey. Within this overarching pattern there are distinct differences among species. Thus, large species handle a certain prey size much faster than small species. However, when further normalizing by predator size, the data for all species (except *Mesocyclops* spp.) collapse on a common relationship. Handling times are generally not limiting maximum consumption rates, and less so for large prey. This allows room for prey selectivity, and indeed copepods are known to be highly selective feeders. Our data predict that copepods can afford to be more selective when feeding on larger than on smaller prey and when consumption is not limited by prey encounter rate, and this is consistent with observations of copepod feeding behavior. We argue that the fast handling times allow copepods to optimize their diet through prey selectivity, and that this is one key to the evolutionary success of pelagic copepods.

Copepods are among the most abundant metazoans on earth, play a pivotal role in biogeochemical cycling (Steinberg and Landry 2017; Serra-Pompei et al. 2022) and are important vectors for the transfer of energy in marine food webs (Sommer et al. 2002; Turner 2004). Pelagic copepods feed in a variety of manners including ambush feeding, feeding-current feeding, and cruise feeding (Kiørboe 2011). Copepods use their feeding appendages to handle the prey prior to, and while ingesting or rejecting it, and during this period the copepod cannot capture another prey (Tiselius et al. 2013). The duration of this period—the prey-handling time (Holling 1959) may be limiting the maximum consumption rate, or the maximum consumption rate may be limited by other factors, for example, the digestion time. The handling time parameter is commonly derived from functional response calculations (Kiørboe et al. 2018), but this parameter includes not only the time to handle prey but also the digestion time (Jeschke et al. 2002). When derived this way the two effects cannot be separated, which can lead to misconceptions about the effect of prey-handling times on ingestion rates (Papanikolaou et al. 2021). Direct observations in a limited number of copepod species have suggested that handling times are short and nonlimiting (Henriksen et al. 2007; Tiselius et al. 2013).

However, prey-handling times may vary between copepods with different feeding modes and are in addition influenced by several prey-related factors. Generally, larger prey take longer to handle and ingest (Rao and Kumar 2002; Tiselius et al. 2013; Gonçalves et al. 2014; Ryderheim et al. 2022*b*), and more recently it was found that diatoms with thicker shells are handled for a significantly longer time than those with thin shells (Ryderheim et al. 2022*a*). Also, copepods are known to be very selective feeders (Teegarden 1999; Leitão et al. 2018) and may handle but reject a large fraction of

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Additional Supporting Information may be found in the online version of this article.

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captured prey, which may thus further detract from the time available for searching new prey (Jeschke et al. 2002). Frost (1972) suggested that more efficient handling of large relative to small prey may explain, at least in part, selective feeding in *Calanus* copepods. Thus, it is still unclear whether and when handling times will affect copepod ingestion rates and have a role in prey selection.

Here, we compile data on prey-handling times in copepods across 10 species and 2 orders to test the hypothesis that handling time limits consumption rates. We explore how preyhandling times vary with predator and prey properties, and we develop a functional response model to examine whether and when prey handling and prey selection can limit ingestion in suspension feeding copepods. We find that preyhandling times vary by five orders of magnitude but that it rarely limits consumption rates. Handling times suggest that it is more efficient for copepods to feed on large rather than small prey and that copepods therefore can afford to be more selective with large prey. However, selectivity limits consumption when encounter limited. The predicted patterns in prey selectivity with prey concentration and prey size are consistent with observations.

#### Materials and methods

#### Data collection

We collected data based on Google Scholar searches on prev-handling times that were based on direct observations of copepod-prey interactions. Data were extracted from tables, digitized from graphs, or acquired directly from the authors. We only included observations that stated whether prey was successfully ingested or rejected, and where size measurements of both copepod and prey were available. We did not include observations where prey or predator properties had been modified to affect handling times (i.e., increased defense, starvation), or where the prey was not fully ingested (Chang and Hanazato 2005a). If literature values were reported as means and individual data points were not available, they were weighted in the model analyses by the number of observations used to compute the mean. If the number of observations were given in a range, we took the average from that range.

In addition to collecting data from the literature, we also analyzed our own unprocessed high-speed videos of preycapture events and videos collected for other means in previous studies. The unprocessed videos were of wild copepods from the Gullmar Fjord, Sweden (*Calanus* sp. and some observations of *Paracalanus parvus* copepodites and adults), or from our own continuous cultures (*Oithona davisae* nauplii). All videos were analyzed using the software ImageJ (National Institutes of Health, USA). Copepod prosome lengths were measured using available pixel-to-length calibrations, while prey sizes were extracted from available data or by measuring 20 individual cells after assigning fitting geometric shapes. Prey-handling time was defined as the time from the copepod reacts until the prey had been ingested or rejected (Tiselius et al. 2013; Gonçalves et al. 2014). In ambush- and cruise-feeding copepods, this also includes the "attack-time," that is, the time it takes the copepod to jump toward and capture the prey (Bruno et al. 2012; Kjellerup and Kiørboe 2012).

#### Data processing

To account for differences in predator and prey sizes, we analyzed handling times as a function of the prey-predator size ratio (vol vol<sup>-1</sup>). Copepod volumes were estimated from length-body volume (Mauchline 1998) or length-carbon relationships (Supporting Information Table S1). Carbon was converted to volume assuming C = 10% of the wet weight (WW) and a density of 1 g WW  $cm^{-3}$  (Kiørboe 2013). Copepod body volumes span four orders of magnitude, from  $\sim 3.5 \times 10^{-4}$  to  $\sim 1.2 \text{ mm}^3$  (O. davisae nauplii and Metridia longa adults, respectively). Prey volumes were estimated from reported values of equivalent spherical diameter, by assigning fitting geometric shapes to reported prey dimensions of individually observed prey captures, or through estimated carbon contents that was transformed to volume (see Supporting Information Tables S2, S3 for more details), and range from small flagellates ( $\sim 140 \,\mu m^3$ ) to fish larvae several times larger than the copepod itself (~  $1 \times 10^9 \,\mu m^3$ ; Supporting Information Appendix S2). Prev volumes for chain-forming diatoms were calculated as cylinders and, thus, may be slightly overestimated.

In total, we collected 656 observations, of which 505 were of ingested prey and 151 of rejected prey (Table 1). The observations include copepods with different feeding modes and life history stages (nauplii, copepodites, and adults). The distribution of relative prey sizes between cyclopoid and calanoid copepods in the data (Fig. 1) reflects their different prey size spectra (Kiørboe 2016). All raw data are available in the supplement (Supporting Information Appendix S2).

The prymnesiophyte Phaeocystis globosa forms spherical colonies that may reach up to cm diameters (Rousseau et al. 2007). The colonies are made up of a mucous-like substance, and, thus, are not "sturdy," as large unicellular prey. Ryderheim et al. (2022b) found that larger colonies of P. globosa takes longer to ingest, but that the copepods in the process squeeze the colonies together, leading to an unknown fraction of the colony being lost in "sloppy feeding." Thus, we will separate these from the analysis of other Temora longicornis capture events that end in prey ingestion, since the handling time here may be underestimated compared to a "rigid" cell or colony of similar size (Jansen 2008). During prey rejechowever, tion, colonies remain intact (Ryderheim et al. 2022b), and we thus include them in this analysis. Complete data on P. globosa can be found in the supplement (Supporting Information Fig. S1).

**Table 1.** Summary of copepod feeding mode, and the number of observations that ended in ingestion or rejection of prey for the different copepod species. All observations are of copepodites and adults, unless otherwise noted. All our *Acartia tonsa* observations are with motile prey, where the copepod feeds via ambush feeding. Length refers to the prosome for adults and copepodites, and the entire body for nauplii.

Species	Length (mm)	Feeding mode	Ing.	Rej.	n	Source
Calanoids						
Acartia tonsa		Ambush				Bruno et al. (2012), Jonsson and Tiselius (1990), Kiørboe et al. (2009)
Adult/copepodite	0.7–0.9		15		15	
Nauplii	0.2		2		2	
Calanus sp.	1.9–2.5	Feeding current	51		51	T. Kiørboe unpubl.
Metridia longa	1.9–3.3	Cruising	17		17	Kjellerup and Kiørboe (2012)
Paracalanus parvus	0.4–0.7	Feeding current	61	56	117	T. Kiørboe unpubl., Tiselius et al. (2013)
Temora longicornis		Feeding current				Bruno et al. (2012), Gonçalves et al. (2014), Olesen et al. (2022), Ryderheim et al. (2022 <i>a</i> , <i>b</i> )
Adult/copepodite	0.6–0.9		225	80	305	
Nauplii	0.2		2		2	
Cyclopoids						
Apocyclops royi	0.6	Ambush	1		1	Zempléni et al. (2022)
Mesocyclops pehpeiensis	0.9	Ambush	4		4	Hwang et al. (2009)
Mesocyclops sp.	1.2–1.5	Ambush	60		60	Chang and Hanazato (2005 <i>a,b</i> ), Sakamoto and Hanazato (2008)
Mesocyclops thermocyclopoides	1	Ambush	39		39	Rao and Kumar (2002), Kumar et al. (2012)
Oithona davisae		Ambush				L. T. Nielsen unpubl.
Adult/copepodite	0.2-0.3		7	1	8	·
Nauplii	0.1–0.2		21	14	35	

Ing, ingestions; n, total number of observations; Rej, rejections.



**Fig 1.** Frequency distribution of handling time observations for different prey : predator size ratios. Data include both prey ingestions and rejections. n = 509 for calanoids, n = 146 for cyclopoids.

#### The effect of temperature on prey handling

Although many feeding-related processes are temperature dependent (Hansen et al. 1997), it is not known how temperature may affect the time it takes copepods to handle prey. Thus, we did not know if temperature adjustments had to be made to compare data collected at different temperatures. To explore this, we recorded the copepod T. longicornis handling prey at three temperatures (18°C, 13°C, and 5°C). These temperatures were chosen as most of our observations of calanoid copepods fall within this temperature range (Supporting Information Appendix S2). Copepods from our lab culture (18°C) were gradually acclimatized to the three temperatures over the course of 10 d. We tethered latestage copepodites or adult T. longicornis females to a human hair by their dorsal surface using super glue, and observed their preyhandling times of the dinoflagellate Alexandrium minutum, as described in Ryderheim et al. (2022b). The video sequences were analyzed using ImageJ, and handling time was defined as above.

#### Functional response model

We explored the scope for prey selection as a function of prey concentration and prey size further by a simple model.

We pose a state-space model for a foraging copepod. The state has two components: (i) stomach fullness, a number between 0 and 1, and (ii) activity, which can be either searching, screening a captured prey for suitability, or handling. Stomach contents are digested according to  $\dot{s} = -rS$ , that is, exponential decay (Kiørboe and Tiselius 1987). When the copepod is searching, prey are encountered at the rate  $\lambda$  (encounters time $^{-1}$ ). The sojourn time in the *screening* state is exponentially distributed with rate  $\tau_{s}$ . The probability of accepting a captured prey is  $p_{\rm H}$ . Accepted prey are handled and the han*dling time* is exponentially distributed with mean  $\tau_{\rm H}$ . Alternatively, the copepod rejects the prey and goes back to searching. At the end of *handling* the prey is ingested if there is room in the stomach. Thus, the handling time of ingested prey in our data is  $\tau_{\rm S} + \tau_{\rm H}$ , and that of rejected prey is  $\tau_{\rm S}$ . After rejecting or handling the prey, the copepod begins searching again. Prey sizes are  $\beta$ -distributed. The parameters in the  $\beta$  distribution are chosen so that the mean prey size is  $m_{\rm F}$ , and the variance is  $S_{R}^{2}m_{F}(1-m_{F})$ . These are all relative to the maximum stomach contents.

#### Statistical analysis

The collected handling time data were analyzed with linear regressions and the effect of temperature on handling time was analyzed with ANOVA. Statistical tests were done using R version 4.2.1 and considered significant at the 0.05 level.

#### Results

We found no effect of ambient temperature on the handling time of ingested prey (Fig. 2); thus, no corrections were made to the data.

Prey-handling times vary by more than five orders of magnitude, from ~ 10 ms to ~ 35 min per prey (Fig. 3A). A large fraction of this variability is accounted for by relative prey sizes, in that larger prey generally require longer handling times than small prey in both calanoid and cyclopoid copepods (Fig. 3A; Supporting Information Fig. S2). However, there are up to one order of magnitude differences between calanoid species in handling times of prey of similar relative sizes, and even larger differences between the cyclopoid species (~ 3 orders of magnitude; Fig. 3B,C).

Handling time normalized by prey size decrease with prey size for all species (Fig. 4A), but again with distinct differences between species that appear to be size-related: the largest calanoids (*Calanus* sp. and *M. longa*) spend the shortest time handling a unit volume of prey (*see* Supporting Information Video S1 for *Calanus* sp. handling of a large dinoflagellate), while the smallest cyclopoids spend three orders of magnitude more time on the same task. The intermediately sized calanoids (*Acartia tonsa, P. parvus,* and *T. longicornis*) have intermediate time spendings. The size (mass) difference between the large calanoids and the small cyclopoids are also about three orders of magnitude, implying that the handling time

Prey handling in copepods



**Fig 2.** The effect of temperature on the handling time of *Temora longicornis* feeding on the dinoflagellate *Alexandrium minutum* at three different temperatures. Data are only for ingested prey. Handling times were normalized by copepod dry weight (DW) to account for differences in size. DW was estimated from the length–weight relationship established by Hay et al. (1991). The large dots show means and error bars are the standard deviation. Small dots show individual observations. We found no significant effect of temperature on the time it took the copepods to ingest cells (ANOVA,  $F_{2,32} = 1.52$ , p = 0.23).

per *relative* volume of prey is about similar for all copepods. Thus, accounting for the differences in predator size reduces the interspecific variability with data for most calanoids and cyclopoids collapsing on a common relationship (Fig. 4B). However, *Mesocyclops* spp. still display significantly longer handling times.

Adult copepods and copepodites handle, on a volumetric basis, prey faster than nauplii (Supporting Information Fig. S3). Looking again at the handling per relative volume of prey suggests that the different stages spend similar times handling smaller prey, but that nauplii are more efficient with larger prey (Supporting Information Fig. S3).

Prey that are rejected subsequent to capture are handled slightly faster than ingested prey in two out of the three species where comparisons were possible ( $\sim 33\%$  in *O. davisae* and  $\sim 56\%$  in *T. longicornis*, respectively; Fig. 5A,C). In the third species, *P. parvus*, rejected prey were handled for  $\sim 77\%$  longer than ingested prey (Fig. 5B).

#### Functional response model

To explore the effect of handling time and prey selectivity on consumption rate by the model we consider a foraging copepod with mass 2  $\mu$ g C. A copepod of this size has a maximum ingestion of approximately 0.5  $\mu$ g C h<sup>-1</sup> (Kiørboe and Hirst 2014), and using a gut turnover rate of 2.4 h<sup>-1</sup> (Kiørboe et al. 1982) we can estimate the stomach size (in carbon



**Fig 3.** Relation between prey-handling time (HT, ms) and prey : predator size ratio ( $\mu$ m<sup>3</sup>  $\mu$ m<sup>-3</sup>) for suspension-feeding copepods. The overall relationship (**A**) is log<sub>10</sub> (HT) = 5.47 + 0.75 × log<sub>10</sub> (ratio);  $R^2 = 0.79$ , p < 0.001. (**B**,**C**) The same data but for individual calanoid and cyclopoid species, respectively. Regression parameters for individual species are found in the Supporting Information (Table S4). Shaded areas are 95% confidence intervals.



**Fig 4.** (A) Volumetric handling time (ms  $\mu$ m<sup>-3</sup>) or (B) size-specific volumetric handling time (ms  $\mu$ m<sup>-3</sup> mm<sup>-3</sup>) as a function of the prey : predator size ratio ( $\mu$ m<sup>3</sup>  $\mu$ m<sup>-3</sup>) for suspension-feeding copepods. Regression parameters are found in the Supporting Information (Table S4). Shaded areas are 95% confidence intervals.

equivalents) as 0.5  $\mu$ g C h<sup>-1</sup>/2.4 h<sup>-1</sup> = 0.2  $\mu$ g C. By estimating the stomach size we can estimate the size of a prey relative to the size of the stomach, that is, how many prey that can fit in the stomach. In our simulations, we assume a food size standard deviation of 10%.

Our functional response model produces saturating curves similar to that of the disc equation (Fig. 6). At low prey densities, the copepod is encounter and selection limited, while at high prey densities (i.e., where  $I = I_{max}$ ) it is always digestion limited. Increased prey-handling time only affects the ingestion at intermediate prey densities but is highly influenced by

the probability to accept prey, that is, the effect is increased at lower accept probabilities (Fig. 6C,D). The effect of a longer handling time is increased with a decrease in prey size (Fig. 6C,D).

#### Discussion

#### Prey size and handling time

The more than five orders of magnitude difference in preyhandling times observed are to a large extent explained by the relative size of the prey: larger prey takes longer to handle but

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**Fig 5.** Volumetric handling time (ms  $\mu$ m<sup>-3</sup>) as a function of the prey : predator size ratio ( $\mu$ m<sup>3</sup>  $\mu$ m<sup>-3</sup>) for (**A**) *Oithona davisae*, (**B**) *Paracalanus parvus*, and (**C**) *Temora longicornis*. *O. davisae* (ANOVA,  $F_{1,39} = 4.3$ , p = 0.045) and *T. longicornis* (ANOVA,  $F_{1,287} = 105.5$ , p < 0.001) both handled rejected prey faster than ingested prey, while the opposite trend was found for *P. parvus* (ANOVA,  $F_{1,14} = 10.2$ , p = 0.002).



**Fig 6.** Model estimations on how ingestion rate varies with different probabilities to accept (**A**,**B**) and the combination of probability to accept and prey-handling times (**C**,**D**). We assume that the copepod feeds on either a 25  $\mu$ m (**A**,**C**) or a 14  $\mu$ m (**B**,**D**) diatom with carbon contents of ~ 4 × 10<sup>-4</sup> and ~ 1.2 × 10<sup>-4</sup>  $\mu$ g cell<sup>-1</sup>, respectively (Menden-Deuer and Lessard 2000) at 16°C. Relative to the maximum stomach size this is equal to 0.0004/0.2 = 0.002 and 0.0004/0.2 = 0.0006, for the larger and smaller cells, respectively. The screening time for all simulations is set to 0.3 s and the gut turnover rate is 0.05 min<sup>-1</sup>. (**A**) and (**B**) show how ingestion vary with the probability to accept prey (i.e., how likely the copepod is to reject a prey or not) with a handling time of 1 s. (**C**) and (**D**) show how increased handling of prey will affect the copepod ingestion at two different probabilities to accept.

are handled faster when expressed per unit prey volume. In addition, large copepods handle prey of similar relative size faster than small copepods.

It is perhaps intuitive that prey-handling times increase with prey size. As a consequence, it has often been suggested that the increased handling time of larger prey will limit feeding or be energetically inefficient for the copepods, for example, when feeding on elongated diatom chains and filamentous cyanobacteria (Vanderploeg et al. 1988; Olson et al. 2006; Rangel et al. 2020). However, elongation does not necessarily interfere with prey handling (Ryderheim et al. 2022*b*), and our data summary demonstrates that feeding on larger prey in fact is more efficient in terms of handling times.

It is maybe more surprising that larger copepods handle prey of a given size-both absolute and relative size-much faster than a small copepod, because it is the same sequence of acts: capture, screening, and rejection or consumption. During handling, the copepod has to first examine (screen) the prey and decide whether or not to eat it and, if accepted, subsequently use the appendages to consume the prey. One would expect the screening part to be size-independent as the chemical and mechanical sensors on the feeding appendages are similar and independent of size. That appears, however, not to be the case (Fig. 5). It is maybe easier to imagine how a relatively large prey requires more time to be manipulated for consumption than a small prey (see Supporting Information Video S2), and that small and large prey are manipulated differently. Thus, Koehl (2004) described how the copepod Eucalanus pileatus move their second maxillae differently depending on whether it is capturing small or large cells, and copepods have to spend time re-orienting chains of diatoms prior to ingestion that they would not have to do with a spherical prey of similar size. In any case, if handling time was independent of the size of the copepod, consumption rates would be severely and increasingly limited by handling time with increasing size of the copepod.

Some of the variation in handling time is species-specific, and the variation between copepod species seems more pronounced than between the different feeding modes (Supporting Information Fig. S4). Thus, T. longicornis spend 10 times longer handling prey of a certain size than similarly sized P. parvus, for example. Within the cyclopoid copepods, the differences are even larger, with Mesocyclops sp. spending three orders of magnitude longer than O. davisae handling prey of similar relative sizes. Although potential prey preferences can often be deduced from differences in the structure of the antennules, feeding appendages, and mandibles (Ohtsuka and Onbé 1991; Michels and Schnack-Schiel 2005), species-specific differences in handling times are not related to morphological differences in any obvious manner. However, some of the variation may relate to differences in properties of the prey (Kalinoski and DeLong 2016). Thus, the majority of Mesocyclops spp. observations are of prey with morphological

properties thought to affect predation, for example, with shells and spines commonly found in cladocerans. This is particularly obvious in Mesocyclops thermocyclopoides, which on a per volume basis spends a similar amount of time handling smaller rotifers and a ciliate as they do on handling largersized Cladocera (Supporting Information Fig. S5A). In addition, diatoms are overall handled longer by T. longicornis adults and copepodites than similarly sized dinoflagellates and ciliates (Supporting Information Fig. S5B). Combined with a lower nutritional content (Jones and Flynn 2005), this may partly explain why copepods seemingly favor dinoflagellates and ciliates over diatoms in their diets (Saiz and Calbet 2011). Some prey may harness a defense in response to the presence of predators' cues (Tollrian 1995; Pondaven et al. 2007), and such defended prey may take longer to handle (not included in our compilation). Thus, thin-shelled cells of diatoms are handled by T. longicornis substantially faster than grazerinduced thick-shelled cells of the same diatom species (Ryderheim et al. 2022a).

# Is prey handling and prey selection limiting consumption rates?

The large differences in prey-handling times may have implications to the foraging ecology of the copepods in terms of whether or not handling times are limiting consumption rates or affecting the time–cost of prey selection. One can assess the potential limiting effect of handling time on consumption rate by comparing the maximum ingestion rate estimated from handling time (i.e., 1/[handling time]) with that estimated from the functional response (Fig. 7; Holling 1959). If the former is larger than the latter, ingestion is limited by other factors, such as the ability of the gut to process the food (Tiselius et al. 2013).

Evidently, maximum ingestion rates are typically not limited by handling time, and least so in calanoid copepods foraging on large prey (Fig. 7). By modeling the ingestion rate through a simple functional response model, we find that that at low food densities the copepod is encounter limited, and always becomes digestion-limited at high densities of food (Fig. 6). That is, the maximum ingestion rate can never exceed the rate at which the food is processes by the stomach. This effect is independent of handling and digestion, and the size of the prey (Frost 1972). Thus, it is only at intermediate densities of food that increased handling times have an effect on the ingestion rate. Thus, if food availability is unlimited, this leaves plenty of room for the copepods to be selective and ingestion seems mainly dependent on the probability to ingest the captured prey (Fig. 6). In fact, copepods are highly selective feeders and may select prey based on its nutritional value (Cowles et al. 1988; Meunier et al. 2016), its contents of toxins (Teegarden 1999; Ryderheim et al. 2021; Olesen et al. 2022), or other properties of the cell (Stemberger 1985; Atkinson 1995; Ryderheim et al. 2022a), and may at times reject > 90% of the prey captured (Xu and Kiørboe 2018).



**Fig 7.** Maximum ingestion rate ( $\mu$ g C h<sup>-1</sup>) as a function of copepod carbon mass (mg C copepod<sup>-1</sup>) in (**A**) calanoid and (**B**) cyclopoid copepods. "Handling  $I_{max}$ " estimated as 1/(handling time), includes only data on ingested prey. Functional response data are from Kiørboe and Hirst (2014). In (**B**), we supplemented their data with additional observations (*see* Supporting Information for details). The different colors indicate different prey sizes: (**A**) yellow, 0–20  $\mu$ m; purple, 20–40  $\mu$ m, magenta; 40+  $\mu$ m, (**B**) yellow, 0–32  $\mu$ m; purple, 32–256  $\mu$ m; magenta, 256+  $\mu$ m. The regression line slopes in (**A**) are not significantly different from one another (p > 0.05). "Handling  $I_{max}$ " regression lines in (**B**) shown only for visual purposes (the fit for small prey is not significantly different from zero, and the two larger prey classes include very little spread in copepod size, thus, we are wary of making predictions).

Foraging on small prey leaves less room for prey selection (Figs. 6, 7A), consistent with the observation that copepods are less selective when feeding on small than when feeding on large prey (Ryderheim et al. 2022*a*) and that copepods feeding on small prey require higher food densities (Frost 1972; Kiørboe et al. 2018). In addition, the impact of increased handling times on ingestion is relatively higher with smaller prey, despite the higher probability to ingest.

#### Conclusions

We demonstrate by means of data analysis and simple mathematical modeling that although prey-handling times in copepods vary by many orders of magnitude, they are rarely limiting consumption rates. This is in contrast to other pelagic suspension feeders, like heterotrophic flagellates, where maximum ingestion rates appear to be handling-time limited (Suzuki-Tellier et al. 2022). This implies that other processes, mainly gut processing times, are limiting maximum ingestion in copepods. The nonlimiting handling times allow copepods to be selective feeders, particularly when prey encounter rates are not limiting. Copepods typically have dome-shaped prev size spectra (Hansen et al. 1994), simply as a result of encounter rate increasing with prey size and the ability to capture and handle prey decreasing with prey size (Greene 1988). However, within this size constraint, copepods may select prev of optimal quality and discard prev of less quality, for example prey of limited nutritional value (Cowles et al. 1988; Meunier et al. 2016), or diatom prey with a thick shell that would unnecessarily tear the mandibles when crushing the prey (Ryderheim et al. 2022*a*). Our handling time observations predict that copepods can afford becoming increasingly selective with the size and concentration of prey, and this is consistent with observations (Ryderheim et al. 2022*a*). Because gut processing times are strongly temperature dependent (Dam and Peterson 1988), while handling times appear not to be (Fig. 2), one can speculate that copepods living at warmer temperatures, where handling-times become increasingly limiting, would be less selective.

There is one notable exception to the prediction of preysize dependent prey selection: when copepods (*T. longicornis*) are offered toxic dinoflagellates, they discard these cells at a rate independent of their concentration, even when offered at low concentrations (Xu et al. 2017). This suggests that it is not only the ability to evaluate prey quality during handling, but also the very short handling times that allow copepods to be picky about their food. This ability helps optimize the nutrition and, hence, performance of copepods, and is yet another reason for the evolutionary success of pelagic copepods.

#### Data availability statement

All data used to draw conclusions and compute figures, and code for the functional response model are available in the supplementary material.

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#### Conflict of interest

None declared.

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