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Swimming behavior and prey retention of the polychaete larvae *Polydora ciliata* (Johnston)

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**SUMMARY**

The behavior of the ubiquitous estuarine planktrophic spionid polychaete larvae *Polydora ciliata* was studied. We describe ontogenetic changes in morphology, swimming speed and feeding rates and have developed a simple swimming model using low Reynolds number hydrodynamics. In the model we assumed that the ciliary swimming apparatus is primarily composed of the prototroch and secondarily by the telotroch. The model predicted swimming speeds and feeding rates that corresponded well with the measured speeds and rates. Applying empirical data to the model, we were able to explain the profound decrease in specific feeding rates and the observed increase in the difference between upward and downward swimming speeds with larval size. We estimated a critical larval length above which the buoyancy-corrected weight of the larva exceeds the propulsion force generated by the ciliary swimming apparatus and thus forces the larva to the bottom. This modeled critical larval length corresponded to approximately 1 mm, at which, according to the literature, competence for metamorphosis and no more length increase is observed. These findings may have general implications for all planktivorous polychaete larvae that feed without trailing threads. We observed bell shaped particle retention spectra with a minimum prey size of approximately 4 μm equivalent spherical diameter, and we found that an ontogenetic increase in maximum prey size add to a reduction in intra-specific food competition in the various larval stages. In a grazing experiment using natural seawater, ciliates were cleared approximately 50% more efficiently than similar sized dinoflagellates. The prey sizes retainable for *P. ciliata* larvae covers the microplankton fraction and includes non-motile as well as motile prey items, which is why the larvae are trophically positioned among the copepods and dinoflagellates. Not only do larval morphology and behavior govern larval feeding, prey behavior also influences the feeding efficiency of *Polydora ciliata*.

Key words: *Polydora ciliata*, low Reynolds number hydrodynamics, swimming behavior, prey selection.

**INTRODUCTION**

Spionid polychaetes are some of the most common benthic invertebrates of neritic environments. Hence, during certain periods, their planktrophic larvae are very abundant in coastal waters. They reach concentrations >1000 l⁻¹ and are a major component of the zooplankton community (Anger et al., 1986; Zajac, 1991; Bochert and Brick, 1996; Pedersen et al., 2008). Spionids are one of the most common and widespread polychaete families in the Oslofjord, Norway (Schram, 1968) and in the Isefjord complex, Denmark (Rasmussen, 1973) from which the present larval material was collected. Among spionids, *Polydora ciliata* is one of the dominant species, with a wide geographic distribution in Northwest Europe, and it is also found in Australian and Japanese waters as an introduced species (NIMPIS, 2002). *P. ciliata* larvae may be the single most dominant polychaete larvae in neritic waters and reach concentrations >500 l⁻¹ and their potential trophic role cannot be neglected (Daro and Polk, 1973, Pedersen et al., 2008; Pedersen et al., 2010).

Fig. 1 shows *P. ciliata* in the early, intermediate, and late larval stage. *Polydora* spp. larval morphology is described in detail by Wilson (Wilson, 1928), Hannertz (Hannertz, 1956), Blake (Blake, 1969) and Plate and Husemann (Plate and Husemann, 1994). Based on the detailed sketches by Wilson (Wilson, 1928), we presume that the ciliary swimming apparatus is primarily composed of a band of closely spaced cilia (the prototroch), surrounding approximately three-quarters of the head circumference, and secondarily by a band of cilia around the terminal segment (the telotroch). Many spionids lack feeding cilia (‘metatroch’) and food groove, and must therefore capture particles using alternative mechanisms (Pernet and McArthur, 2006). This is most likely the case for *P. ciliata* larvae.

Data on particle size retention in polychaete larvae are scarce. For example, the upper limit for ingestible particle size increased with larval size for *Streblospi benedicti* (Pernet and McArthur, 2006) and also for a gastropod veliger. For the gastropod veliger it was simply explained by changes in morphological dimensions of the feeding apparatus (velum structures) (Hansen, 1991). The linkage between particle retention mechanism and the morphology of the ciliary feeding apparatus are not reported for *Polydora* larvae. In the spionid *Marenzelleria cf. viridis* phytoplankton <20 μm were the principal dietary component and a maximum prey diameter of 80 μm is described for larvae with 6–10 segments (setigers) (Burckhart et al., 1997). *Polydora* has been reported to have been rearred on microalgae (Anger et al., 1986), and Daro and Polk (Daro and Polk, 2003) reported small phytoplankton and even invertebrates of neritic environments. Hence, during certain periods, Spionid polychaetes are some of the most common benthic invertebrates of neritic environments. Hence, during certain periods
interpretation of the observed development in ontogenetic swimming behaviors we developed a simple swimming model based on low Reynolds number hydrodynamics. Using the modeling approach we further interpreted our observations of the maximum clearance rate and its dependence on larval size. Thus our aim was to explore the interaction between functional morphology and behavioral components in spionid larval suspension feeding.

MATERIALS AND METHODS
Larval collection
Live zooplankton was collected from surface water (0–2.5 m) with a 50 μm WP-2 net equipped with a non-filtering cod-end by horizontal trawling at slow speed. The sampling station ‘Søminestationen’ (55°44′/H11032′′N, 11°48′/H11032′′E) is situated in the Isefjord, Denmark, and it is shallow with muddy bottom sediments and eutrophic waters. Once the net was retrieved, zooplankton was gently transferred to an isothermic container, diluted with surface water, and transported to the laboratory within 2 h of collection. In the laboratory, *P. ciliata* larvae were concentrated using a cold fiber optic light source, sorted with a pipette under the dissecting microscope and placed in a beaker with 0.2 μm filtered seawater (FSW) from the sampling area. In order to reduce contamination by other planktonic organisms, the larvae were washed repeatedly by transferring them through a series of Petri dishes with 0.2 μm FSW until ambient phytoplankton were absent.

Swimming behavior
Swimming of *P. ciliata* larvae (*N*=58) of various lengths was studied in a 15×15×15 cm³ acrylic aquarium at a temperature of 20°C and a salinity of 15 PSU. The setup allowed us to visualize swimming trajectories spatially and estimate true three-dimensional swimming velocities and behaviors. Briefly, a mirror was mounted transversely inside the aquarium allowing direct observations of larvae and their mirrored images simultaneously. Illumination was provided by an infrared light-emitting diode placed perpendicular to the camera. The diode was positioned in the focal point of a Fresnel lens (diameter 16 cm), thus creating parallel (collimated) light beams in the experimental aquarium and in turn mirrored into a monochrome analogue CCD video camera (Minitron MTV-1802CD, Minitron Enterprise Company, Taipei, Taiwan) fitted with a 105 mm lens. Size calibration was done by filming a ruler and converting pixels to millimeters. Video observations were recorded on a VHS tape recorder. After recording the video sequences of interest were digitized using a Pinnacle movie box™ (Pinnacle Systems, Mountain View, CA, USA) into QuickTime™. Movies and motion tracks were analyzed using a motion analysis software package (LabTrack, Bioras.dk, Nivå, Denmark). After the motion tracks were digitized, three-dimensional tracks were reconstructed by merging each motion track with the mirror track manually. Larval swimming was studied in three prey regimes: filtered seawater, filtered seawater with *Rhodomonas salina* added as small prey, and filtered seawater 

### Table 1. *Polydora ciliata* larval swimming speed in three different prey regimes

<table>
<thead>
<tr>
<th>Prey species (size, ESD)</th>
<th>$V_{down}$ (mm s⁻¹ ± s.d.)</th>
<th>N</th>
<th>$V_{up}$ (mm s⁻¹ ± s.d.)</th>
<th>N</th>
<th>$V$ (mm s⁻¹ ± s.d.)</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Filtered seawater</td>
<td>1.03±0.39</td>
<td>5</td>
<td>0.43±0.11</td>
<td>4</td>
<td>0.66±0.25</td>
<td>2</td>
</tr>
<tr>
<td><em>Rhodomonas salina</em> (9 μm)</td>
<td>0.82±0.46</td>
<td>16</td>
<td>0.35±0.22</td>
<td>8</td>
<td>0.45±0.10</td>
<td>9</td>
</tr>
<tr>
<td><em>Akashiwo sanguinea</em> (53 μm)</td>
<td>1.02±0.43</td>
<td>15</td>
<td>0.46±0.19</td>
<td>12</td>
<td>0.62±0.19</td>
<td>8</td>
</tr>
</tbody>
</table>

ESD, equivalent spherical diameter.
with *Akashiwo sanguinea* added as large prey (Table 1). Length and diameter of live animals (*N*=57) were estimated from size-calibrated video frames in the software package ImageJ (http://rsbweb.nih.gov/ij/index.html).

**Cilia measurements**

A sub-sample of (*N*=25) live larvae of a wide range of development sizes was sedated with a few drops of MgCl₂ in a small 4 mm deep micro-well and lengths of the prototroch, the telotroch and the larval body were measured. Larvae were separated in three groups according to size (Table 2). The MgCl₂ was applied until the larvae ceased moving. Apart from inducing body shrinkage, MgCl₂ seemed not to damage the larvae, as they recovered after a short period of time and resumed swimming. The larvae were photographed under a microscope at 100× magnification and the images were subsequently analyzed using the software package ImageJ.

**Maximum clearance and ingestion rates**

The functional response for three different development stages of *P. ciliata* larvae fed the diatom *Thalassiosira weissflogii* was determined. The full data-sets are presented elsewhere (Almeda et al., 2009). Larvae were separated into three groups according to size (Table 2). Subsamples of larvae from each size group (*N*=25–30) were fixed in 5% acid lugol solution, and the average lengths and numbers of setigers were determined using an inverted microscope. Initial grazing trials with aged tank seawater turned out unsuccessfully and instead setigers were determined using an inverted microscope. Initial grazing trials was counted by leaving the CSFC sample suction tube directly around 0.5 ml samples in triplicate. The prey cell in the experimental trials was counted by leaving the CSFC sample suction tube directly into the incubation bottles. During counting, the trial bottles were carefully stirred with a mechanical stirrer set at the lowest r.p.m. Prior to starting a series of grazing trials, we compared the counting performance of CSFC to the electronic particle counter and found no significant deviation between the instruments (Almeda et al., 2009). Clearance and ingestion rates were calculated for each food concentration according to Frost (Frost, 1972) after the verification that prey growth rates in grazing bottles were significantly lower than in the prey growth controls (one-way ANOVA, *P*<0.05) and the maximum rates derived from the functional response equations.

**Particle size selection**

We conducted experiments to examine larval feeding efficiency as a function of particle size for early and late larval stages. The two stages were separated from collected larvae according to their size. Larvae were offered potential prey of different size (ESD) ranging from 4 to 53 μm (Table 3). Otherwise the experimental procedure was as described above. The experiments were performed with one phytoplankton species per experimental treatment and with an equal initial phytoplankton biomass (0.2 μg C ml⁻¹ and 1 μg C ml⁻¹ for early and late larval stages, respectively). The prey retention efficiencies of air bubbles. Bottles were incubated for 24 h on a slowly rotating plankton wheel (0.5 r.p.m.) in a temperature-controlled room at 16°C and constant dim light (<5 μmol photons m⁻² s⁻¹).

Cell concentrations in grazing and control trials were determined by a CytoBuoy scanning flow cytometer (CSFC; CytoBuoy b.v., Woerden, The Netherlands). The CSFC is designed to process live phytoplankton particles larger than 1 μm. In this study we counted around 0.5 ml samples in triplicate. The prey cell in the experimental trials was counted by leaving the CSFC sample suction tube directly into the incubation bottles. During counting, the trial bottles were carefully stirred with a mechanical stirrer set at the lowest r.p.m. Prior to starting a series of grazing trials, we compared the counting performance of CSFC to the electronic particle counter and found no significant deviation between the instruments (Almeda et al., 2009). Clearance and ingestion rates were calculated for each food concentration according to Frost (Frost, 1972) after the verification that prey growth rates in grazing bottles were significantly lower than in the prey growth controls (one-way ANOVA, *P*<0.05) and the maximum rates derived from the functional response equations.

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**Phytoplankton species used in the prey size selection experiment and their dimensions**

<table>
<thead>
<tr>
<th>Phytoplankton species</th>
<th>ESD (μm)</th>
<th>Cell volume (μm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isochrysis galbana</td>
<td>4</td>
<td>34</td>
</tr>
<tr>
<td>Rhodomonas salina</td>
<td>9</td>
<td>357</td>
</tr>
<tr>
<td>Thalassiosira weissflogii</td>
<td>13</td>
<td>1124</td>
</tr>
<tr>
<td>Heterocapsa triquetera</td>
<td>19</td>
<td>3591</td>
</tr>
<tr>
<td>Akashiwo sanguinea</td>
<td>53</td>
<td>79,730</td>
</tr>
</tbody>
</table>

Table 3. Phytoplankton species used in the prey size selection experiment and their dimensions.

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Table 2. Characteristics of the *Polydora ciliata* larval stages used in the feeding experiments

<table>
<thead>
<tr>
<th>Larval stage</th>
<th>Length (μm)</th>
<th>Number of setigers</th>
<th>Biomass (μg C)**</th>
<th>Prototroch cilia length (μm)</th>
<th>Telotroch cilia length (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>220±18</td>
<td>3.5±0.8</td>
<td>0.270</td>
<td>26.8±1</td>
<td>25±8</td>
</tr>
<tr>
<td>Intermediate</td>
<td>561±27</td>
<td>8.9±1.7</td>
<td>0.982</td>
<td>44.5±8</td>
<td>32.3±8.8</td>
</tr>
<tr>
<td>Late**</td>
<td>919±16</td>
<td>13.3±1.9</td>
<td>1.941</td>
<td>48.1±3</td>
<td>32.3±11</td>
</tr>
</tbody>
</table>

*With palps. **Larval carbon biomass was calculated based on length (Hansen, 1999). Values are means ± s.d.

Fig. 2. Morphometric relationships of *Polydora ciliata* larvae. Larval circumference (prototroch cilia band length) is plotted versus larval body length (white circles; left axis), and larval body volume is plotted versus larval body length (black circles; right axis).
The experiments consisted of incubations of natural microplanktonic communities with the addition of *P. ciliata* larvae for the experimental treatments. Natural seawater (NSW) for grazing incubations was collected at 1 m depth with a Niskin bottle and screened through a 200 μm mesh by reverse filtration in order to exclude mesozooplankton. The water was amended with a nutrient mixture to compensate for nutrient enrichment due to larval excretion. Twelve 70 ml blue cap bottles were filled with NSW. Then 75 late-stage larvae approximately 900 μm long, were added to six of the NSW-containing bottles. Two bottles with larvae and two without larvae were fixed with 1% acidic Lugol’s solution to determine the initial microplankton abundance. The remaining eight bottles consisting of four grazing bottles and four control bottles were incubated for 24 h on a plankton wheel (0.5 r.p.m.) in a temperature-controlled room at 16°C and constant dim light. Ciliate, dinoflagellate and diatom abundance was estimated by settling 10 ml aliquots in Utermöhl chambers for 24 h in two replicates per treatment and counted under an inverted microscope. Digital images of each cell type were taken and sized with the open source software package ImageJ. Cell volumes were converted into carbon content using a factor of 0.19 pg C μm⁻³ (Putt and Stoecker, 1989) whereas the carbon of dinoflagellates and diatoms was estimated accordingly to the recommendations of Menden-Deuer and Lessard (Menden-Deuer and Lessard, 2000). Grazing was calculated if prey types in grazing trails were significantly different from controls (one-way ANOVA, *P*<0.05). Clearance and ingestion rates were calculated for each prey type according to Frost (Frost, 1972).

**Grazing on natural prey**

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**RESULTS**

**Morphometrics of live larvae**

The body length (*l*) of the larvae that we used for motion analysis ranged from 0.3 mm to 1.0 mm (Fig. 2). The diameter of the larval head and hence the circumference of the prototroch cilia band increased as the larval body length increased. The number of setigers increased from typically three to 13 during growth (Fig. 1 and Table 2). The diameter of the larval (*d*) ranged from 0.16 mm to 0.26 mm and *l/d* increased by a factor of two during growth from *l/d* = 1.9 on average for the early larval stage to *l/d* = 3.8 on average for the late larval stage and hence the larvae did not grow isometrically (Fig. 2). The prototroch cilia were of comparable length in the intermediate and late larval stages and in these stages the cilia were significantly longer than the cilia in the early stage (one-way ANOVA, *P*<0.001; Table 2). The telotroch cilia, however, seemed not to increase in length significantly during larval ontogeny and remained statistically invariant during the larval development (one-way ANOVA, *P* = 0.356).

**Swimming patterns and speeds**

The larvae were swimming in helical paths and showed large individual variations (Fig. 3). A typical swimming path is a sequence of downwards, upwards, and horizontal trajectories. We tested swimming speed of the general swimming groups, i.e. horizontal, downwards and upwards swimming against prey and filtered seawater and found no significant differences in the swimming speed when different prey was offered (one-way ANOVA, *P* > 0.05; Table 1). Furthermore we did not see any differences in swimming pattern and the data sets were pooled into one data set consisting of swimming paths divided into three groups based on the overall swimming direction: horizontal, downwards and upwards swimming. The average of all our measured horizontal swimming speeds (Ve) is 0.50 ±0.21 mm s⁻¹ and we observed that the average...
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**Swimming model**

In our hydrodynamic model we assumed that each individual larva swims lengthwise with constant velocity due to the propulsion force generated by the ciliary swimming apparatus, and that the propulsion force is balanced by the drag on the larval body. We will not attempt to describe the helical swimming paths of the larvae, but only the observed average swimming speed. For simplicity we model the cigar shaped body of the larva as a prolate spheroid with polar radius $a=body\ length/2$ and equatorial radius $b=body\ diameter/2$.

From the measured body lengths ($l$) and horizontal swimming speeds ($V$) we can estimate the Reynolds number of the flow past the swimming larvae. We define the Reynolds number as:

$$Re = \frac{\rho l V}{\eta}, \quad (1)$$

where $\rho$ is the density of the water and $\eta$ is the dynamic viscosity. For the larvae that swim horizontally we find that the Reynolds number ranges from $Re=0.12$ to $Re=0.46$. Since the typical Reynolds number is fairly low, it is a reasonable approximation to model the flow using Stokes’ equation. The drag $D$ on the larva is therefore proportional to both the larval size and the swimming speed:

$$D = C_D \eta a V, \quad (2)$$

where $C_D$ is a dimensionless drag coefficient that only depends on the geometrical shape of the larva. The drag $D$ on a prolate spheroid with polar radius $a$ and equatorial radius $b$, which is moving lengthwise with constant speed at low Reynolds number is [see Happel and Brenner (Happel and Brenner, 1983), pp. 154-156]:

$$D = \frac{8 \pi \eta c V}{(\tau_0^2 + 1)\coth^{-1}\tau_0}, \quad (3)$$

where $c$ is a geometrical parameter that is defined in the following way:

$$c = \sqrt{a^2 - b^2}, \quad (4)$$

and where $\tau_0$ is another geometrical parameter with the definition:

$$\tau_0 = a/c. \quad (5)$$

Eqn 3 is exact and valid for all values of $a/b$, i.e. it is valid for both prolate spheroids with low $a/b$ and slender prolate spheroids with high $a/b$. To explore the drag model for $a/b$ in the range between 2 and 4, which is relevant for *P. ciliata* larvae, we would like to have a more simple analytical expression to work with than the exact Eqn 3. The often-used slender spheroid approximation [see Happel and Brenner (Happel and Brenner, 1983), p. 156; and Berg (Berg, 1993), pp. 55-58]:

$$D = \frac{4 \pi \eta a V}{\ln(2a/b) - 1/2}, \quad (6)$$

is not applicable in the present study, since it overestimates the drag considerably in the $a/b$ range from 2 to 4 and is only a valid approximation of Eqn 3 when $a/b$ is larger than 10. Instead we consider the following approximation [see White (White, 2006), pp. 171-172]:

$$D = \frac{6 \pi (4 + a/b) \eta b V}{5}. \quad (7)$$

Eqn 7 gives a good approximation with less than 1% relative error in the $a/b$ ratio range from 2 to 4 in comparison with the exact drag expression (Eqn 3), and since approximation (Eqn 7) is easy to work with and analyze we shall use it in the following. Inserting Eqn 7 into Eqn 2 and rearranging, we see that the drag coefficient becomes:

$$C_D = \frac{6 \pi (4 + a/b)}{5 a/b}, \quad (8)$$

which decreases from $C_D(3/5)\pi$ with $a/b=2$ (early larval stage) to $C_D=(2/5)\pi$ with $a/b=4$ (late larval stage). We note for comparison the well-known result that $C_D=6\pi$ for a sphere.

The propulsion force $F$ and the drag force $D$ must have the same magnitude if the larva swims with constant velocity. We presume that the ciliary swimming apparatus consists primarily of the prototroch and secondarily of the telotroch cilia band. We do not have detailed observations of the metachronal wave motion in the cilia bands, and we therefore make some simplifying assumptions about the propulsion force. In the following we assume that $F$ is proportional to the length of the cilia bands as suggested by Hansen (Hansen, 1991) and we model the strength of the total cilia force as:

$$F = 2 \pi C_F \eta b U, \quad (9)$$

where $C_F$ is a dimensionless propulsion force coefficient that depends on geometry and distribution of the cilia and $U$ is an effective time-averaged speed of the cilia motion. The propulsion force per unit cilia band length most likely increases as the larva grows and each cilium gets longer, but for simplicity we assume that $C_F \eta U$ is constant during the larval development. By balancing...
the propulsion force $F$ and the drag force $D$ we obtain the swimming speed:

$$V = \frac{5 C_F U}{3 (4 + a/b)} .$$

(10)

The simple model (Eqn10) predicts a slow decrease of the swimming speed in agreement with the observed horizontal swimming speeds (Fig.4). Our fit of Eqn10 to the measured horizontal swimming speeds determines the propulsion force per unit cilia band length to $C_F \eta U = 2.0 \times 10^{-6} \text{N m}^{-1}$, where we have used $\eta = 1.00 \times 10^{-3} \text{Pa s}$ and $a/b$ from our fit to the morphometrics of live larvae (Fig.2).

### Influence of gravity on swimming behavior

The larvae are slightly negatively buoyant, and the upward swimming speed $V_{up}$ is therefore smaller than the downward swimming speed $V_{down}$ (Table 1 and Fig.4). In addition to the propulsion force $F$ and the drag force $D$, the larvae are influenced by gravity, i.e. the buoyancy-corrected weight $m' g$, where $m'$ is the buoyancy-corrected mass of the larva and $g$ denotes the acceleration due to gravity. If we again model the larva body as a prolate spheroid we have:

$$m' = \frac{4}{3} \pi (\rho_s - \rho) a b^2 .$$

(11)

where $\rho_s$ is the average density of the larva. The larva will evidently sink to the bottom if $m' g$ is larger than $F$. The buoyancy-corrected weight grows cubically with size, and if the propulsion force grows linearly with size, there will be a critical maximum body length $l_{max}$ for which $F$ and $m' g$ have the same magnitude. When the larva exceeds the critical body length, gravity will ultimately force the animal towards the sea floor. Using Eqs 9 and 11 and the force balance $F=m' g$ we obtain the following expression:

$$l_{max} = \sqrt{\frac{6 (l_{max} / d_{max}) C_F \eta U}{(\rho_s - \rho) g}} .$$

(12)

Eqn 12 shows that the maximum larval body length $l_{max}$ increases as the square root of the propulsion force per unit length of the cilia band $C_F \eta U$ and decreases as one over the square root of the excess density $\rho_s - \rho$. To compare the model with observations we plotted $F$ and $m' g$ versus larval body length ($l$) using the excess density $\rho_s - \rho = 5 \text{kg m}^{-3}$, $g = 9.8 \text{m s}^{-2}$, $l/d$ from our fit of the morphometrics of live larvae (Fig.2), and $C_F \eta U = 2.0 \times 10^{-6} \text{N m}^{-1}$ from our fit of the horizontal swimming speeds (Fig.4). The propulsion force is large compared with the buoyancy-corrected weight at small body length, whereas the reverse is true at large body length (Fig.5). Using the above parameters we find the maximum larval body length $l_{max} = 0.95 \text{mm}$ in good agreement with the observed body lengths for the largest free swimming larvae reported in nature. We return to the value of the excess density in the Discussion.

### Maximum clearance and ingestion rates

The maximum clearance rate $Q_{max}$ increased approximately proportionally to the larval body length, and the body volume specific clearance rate therefore showed a dramatic 10-fold decrease from $10^5 \text{body volume h}^{-1}$ in the early larval stage to

![Fig. 5. Theoretical curves for propulsion force $F$ (solid line) and buoyancy-corrected weight $m' g$ (dashed line) versus larval body length of Polydora ciliata. Note that the critical larval body length, $l_{max}$, corresponds to the point where the curves for $F$ and $m' g$ intersect.](image)

![Fig. 6. Maximum clearance rate of Polydora ciliata larvae plotted versus larval body length. Black circles (left axis) show the maximum clearance rate (ml larva$^{-1}$ day$^{-1}$); white circles (right axis) show the body volume specific clearance rate (body volume h$^{-1}$). Error bars indicate ±s.d. Open triangles show the model of the maximum clearance rate (Eqn14).](image)

![Fig. 7. Maximum ingestion rate of Polydora ciliata larvae plotted versus larval body length. Black circles (left axis) show the maximum ingestion rate (cell larva$^{-1}$ day$^{-1}$); white circles (right axis) show the body volume specific ingestion rate (body volume day$^{-1}$). Error bars indicate ±s.d.](image)
10⁴ body volume h⁻¹ found in the late larval stage (Fig. 6). The same characteristics are exhibited by the maximum ingestion rate $Q_{\text{max}}$ that increased from approximately $2 \times 10^4$ Thalassiosira weissflogii cells per larva per day to approximately $10^5$ T. weissflogii cells per larva per day. A dramatic decrease in the body volume specific ingestion rate, similar to the decrease in the body volume specific clearance rate was likewise observed (Fig. 7).

To better understand the observed trends of the maximum clearance rate $Q_{\text{max}}$ we modeled it as the product of the clearance area and the swimming speed of the larva:

$$Q_{\text{max}} = \pi \alpha (2b + l_c) l_c V,$$

(13)

where we have used $l_c$ to denote the prototroch cilia length and where the dimensionless number $\alpha$ is used to take into account that the prototroch does not encircle the larva completely. Using the model expression for the swimming speed in Eqn 10 we obtain the expression:

$$Q_{\text{max}} = \frac{5 \pi \alpha C_F (2b + l_c) l_c U}{3 (4 + a/b)}.$$ 

(14)

Our observations of the prototroch cilia length, $l_c$, for the various larval stages gave $l_c=27\mu m$ for the early stage, $l_c=45\mu m$ for the intermediate stage, and $l_c=48\mu m$ for the late stage (Table 2). With these values for $l_c$ in the three larval stages and $\alpha=0.75$ as suggested from sketches by Wilson (Wilson, 1928), we find that the model of $Q_{\text{max}}$ using Eqn 14 overestimates the measured maximum clearance rate for the early stage, agrees well with the measured maximum clearance rate for the intermediate stage, and underestimates the measured maximum clearance rate for the late stage (Fig. 6).

Particle size selection

The larvae of $P. \text{ciliata}$ are able to feed on prey ranging in size from 4µm to 53µm (Fig. 8). Clearance rates varied with prey size and larval length. The early larval stage displayed a maximum retention (optimal prey size) for particles of 12.9µm and showed a reduced retention for smaller and larger particles. The late larval stage retention increased with particle size until a maximum somewhere between 19µm and 53µm was reached.

Grazing on natural prey

The protist plankton community was initially dominated by the dinoflagellate Heterocapsa triquetra with more than 400 cells ml⁻¹, and its abundance exceeded the abundance of ciliates of approximately 4 cells ml⁻¹ with a factor of 100. The ciliate community consisted mainly of Strombidium spp. Diatoms were scarce with only 0.1 cells ml⁻¹ and they consisted mainly of Ditylum cf. brightwellii and Coscinodiscus spp. Feeding rates on dinoflagellates and ciliates are shown in Table 4. The dominance of H. triquetra made dinoflagellates the most important source of food for $P. \text{ciliata}$ in this situation. However, ciliates that made a much less abundant food source were in fact cleared at a rate that was 2.5-fold higher than the clearance rate on H. triquetra.

DISCUSSION

Swimming patterns and speeds

No systematic differences in the patterns of the swimming paths related to larval size or food particle regime were observed, and we found similar swimming paths even when the larvae were exposed to 0.2µm filtered seawater. Earlier observations, which were interpreted as raptorial feeding behavior, are most likely reactions to physical obstruction by a large particle as shown for gastropod veligers and calanoid copepodites (Hansen et al., 1991). Moreover, at any given larval development stage, the larval swimming paths of individuals were very variable (Fig. 3). This is also described by Wilson (Wilson, 1928) where the larvae frequently swims slowly rotating on their longitudinal axes, sometimes in circles about one place, and sometimes they curl up and erect their body spines when disturbed. We have speculated that the adaptive significance of an apparently non-predictable swimming path besides the spine erection could be a means of predator avoidance, but this remains to be verified.

The horizontal swimming speed decreases slowly with body length, which indicates that the propulsion force due to the ciliary swimming apparatus increases slower with body length than the drag on the body. Wilson (Wilson, 1928) suggested that body spines contribute negligibly to the drag, and that the notochord moderately or not at all contributes to the swimming force. Hence, we modeled the propulsion force as generated by the prototroch and the telotroch.

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Table 4. Clearance and ingestion rates obtained in Polydora ciliata larval incubation experiments in natural seawater (Isfjorden)

<table>
<thead>
<tr>
<th>Property</th>
<th>Dinoflagellates</th>
<th>Ciliates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial concentration (cells ml⁻¹)</td>
<td>411±45</td>
<td>4.04±0.74</td>
</tr>
<tr>
<td>Initial biomass (µg C ml⁻¹)</td>
<td>4745±132</td>
<td>2969±65</td>
</tr>
<tr>
<td>Avg. Biomass (ng C ml⁻¹)</td>
<td>0.77±0.02</td>
<td>10.09±0.03</td>
</tr>
<tr>
<td>Clearance rates (ml larva⁻¹ day⁻¹)</td>
<td>1.06±0.13</td>
<td>2.65±0.268</td>
</tr>
<tr>
<td>Ingestion rates (cells larva⁻¹ day⁻¹)</td>
<td>277±19</td>
<td>3.5±0.1</td>
</tr>
<tr>
<td>Clearance rates (ml larva⁻¹ day⁻¹)*</td>
<td>1.17±0.12</td>
<td>3.08±0.37</td>
</tr>
<tr>
<td>Ingestion rates (µg C larva⁻¹ day⁻¹)</td>
<td>0.224±0.012</td>
<td>0.037±0.001</td>
</tr>
<tr>
<td>Carbon specific ingestion (% day⁻¹)</td>
<td>13.0±0.7</td>
<td>2.15±0.05</td>
</tr>
<tr>
<td>Volume specific ingestion (% day⁻¹)</td>
<td>5.4±0.3</td>
<td>0.045±0.004</td>
</tr>
</tbody>
</table>

Values are based on the most abundant prey groups found. Note that clearance values marked with an asterisk are based on the per capita change in cell numbers whereas unmarked clearance rates are calculated from changes in prey biomass. Values are means±s.d.
solely. The decrease of the measured average horizontal speed is well described by the simple swimming model (Eqs 10 and 4) which takes into account that the larvae become relatively more slender (Figs 1 and 2) during their ontogenetic development. However, we speculate that our fit $C_F U^2 \approx 2 \times 10^{-8} \text{Nm}^{-1}$ may be an underestimate of the cilia force per unit length of the cilia band, and also that the cilia force per unit length is not constant but increases slowly throughout larval development as each ciliation gets longer. There are two main reasons for the possible underestimate of the propulsion force. First, in the simple model we balance the propulsion force due to the cilia swimming apparatus by the drag on a passively sinking prolate spheroid. In general the flow around a freely swimming larva is different from the flow around a passively sinking larva, and we note that our modeling approach does not take this into account. Langlois et al. (Langlois et al., 2009) considered a simple model of a self-propelled flagellate consisting of a spherical body with a cylindrical flagellum, and showed that the drag on the body is larger for a self-propelled flagellate relative to the drag on a passively sinking sphere. We presume that our estimate of the propulsion force for the swimming larvae similarly underestimates the true propulsion force, since we do not take into account the increase of the flow speed near the larval body due to the beating cilia. Second, the drag on the larval body may be larger than the prediction obtained from the prolate spheroid expression in Eqn 3, since this expression is derived for an object with a smooth surface and ignores the rough surface and setae structures on the larval body. This could lead to an underestimate of the propulsion force. Presumably this effect is more pronounced in the late larval stage, since the larvae at this stage begin to develop large palps (Fig. 1). Both a detailed morphological description of the cilia band structures and close observations of the metachronal wave of the beating cilia in swimming larvae in combination with direct numerical simulations of the flow past the larva would be needed to fully address these issues.

Planktotrophic larvae display actively phototactic behavior after hatching and this is also described for P. ciliata (Wilson, 1928). This is an adaptation to swim towards the photic zone of the water column where phytoplankton availability is highest. Later when approaching competence for metamorphosis they become negatively phototactic, which is interpreted as an adaptation to seeking the particle capture is by the prototroch and maybe more ciliary structures in combination as described by Strathmann (Strathmann, 1971) and Hart (Hart, 1996). The measured maximum clearance rates are described reasonably well by Eqn 14, using 27 $\mu$m as the prototroch cilia length ($l_c$) for the early larval stage, 45 $\mu$m for the intermediate larval stage, and 48 $\mu$m for the late larval stage (Table 2; Fig. 6). The maximum clearance rate $Q_{\text{max}}$ increased approximately proportionally to the larval body length, and the body volume specific clearance rate therefore showed a dramatic 10-fold decrease. Increasing clearance and ingestion rates as well as increasing optimal prey size has been demonstrated for crustaceans, e.g. the shrimp Sergestes similis and the copepod Acartia tonsa (Omori, 1979; Berggreen et al., 1988). However, specific food uptake rates declined with body weight (Omori, 1979) and optimal prey size remained constant for a ciliated gastropod veliger (Hansen and Ockelmann, 1991). Moreover, a thorough compilation of 13 echinoderm larval species reveals a substantial variation in feeding capabilities among larvae of similar size and shows that some are better suspension feeders than the others. Hence, no clear pattern in size-related clearance rate was detected (Hart, 1996).

**Particle size selection**

The ontogenetic retention spectrum exhibits a constant sized minimum prey, an increased optimal prey size and also an increased maximum prey size with larval body size. This is most probably related to the morphological constraints and the ontogenetic changes in the ciliary apparatus (Hansen, 1991; Risgaard et al., 2000). However, in contrast to the opposed band veliger the maximum prey size for late P. ciliata larvae seems to be larger, which is...
Swimming behavior of *P. ciliata*

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**REFERENCES**


