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Swimming kinematics of *Eurytemora affinis* (Copepoda, Calanoida) reproductive stages and differential vulnerability to predation of larval *Dicentrarchus labrax* (Teleostei, Perciformes)

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In egg-bearing copepods, the ovigerous females are reported to be more vulnerable to predators. However, the underlying mechanistic details of increased vulnerability are not yet well understood. We studied the predator–prey interaction between the copepod prey *Eurytemora affinis* and a predator, post-larvae of the sea bass *Dicentrarchus labrax*. Standard video techniques have been used to quantify the predation efficiency of larval sea bass and to record the two-dimensional swimming behavior of the different reproductive stages (males, non-ovigerous females and ovigerous females) of *E. affinis* in both the absence and presence of predators. Our results revealed that ovigerous females suffered higher mortality rates than either non-ovigerous females or males. Body size and swimming speed seemed to be the main determinants of prey conspicuousness to predators. In the light of published data, we conclude that acute vulnerability of *E. affinis* ovigerous females to planktivorous predators is not necessarily harmful at the population level.

KEYWORDS: predation; *Eurytemora affinis*; *Dicentrarchus labrax*; swimming behavior; acceleration

INTRODUCTION

The role of predators in structuring zooplankton communities has been well documented (e.g. Lazzaro, 1987). Differential predation pressure has been shown not only to affect prey population dynamics, but also to trigger morphological and behavioral evolutionary processes (Kerfoot, 1977). In the natural environment,

trophic level interactions occur at the individual level rather than at the level of whole populations (Kjørboe, 2008). Investigating predator–prey interactions at the individual level seems therefore essential for a better understanding of zooplankton prey dynamics.

In the mega-tidal Seine estuary (English Channel, France), the copepod *Eurytemora affinis* is one of the

dominant mesozooplankton species (Devreker *et al.*, 2008). In this area, it has been reported to be one of the main food sources for juveniles of the European sea bass *Dicentrarchus labrax* (Linnaeus, 1758) (Mouny *et al.*, 1998). Like in many other egg-carrying copepod species (Hairston *et al.*, 1983; Svensson, 1992), ovigerous female *E. affinis* have been reported to be more vulnerable to predation than non-ovigerous females or males (Sandstrom, 1980; Vuorinen *et al.*, 1983). Sandstrom (Sandstrom, 1980) hypothesized that the presence of highly pigmented eggs not only facilitates detection of *E. affinis* by predators, but also hampers their escape responses. For the freshwater genus *Eudiaptomus*, the selection of ovigerous females by predators was attributed to their bigger size and lower escape abilities (Svensson, 1992, 1997a,b). For *E. affinis* in the Seine estuary, where both high turbidity and low light penetration limit vision, the underlying mechanisms behind the enhanced vulnerability of ovigerous females are yet to be investigated. In fact, while the different reproductive stages (males, non-ovigerous females and ovigerous females) of *E. affinis* from the Seine estuary exhibit different swimming patterns (Seuront, 2006; Michalec *et al.*, 2010), the copepods' movements are known to enhance their vulnerability to predators (e.g. Meng and Orsi, 1991). In addition, *D. labrax*, one of the main predators of *E. affinis* in the Seine estuary (Mouny *et al.*, 1998; Mouny and Dauvin, 2002), has a retina with a high concentration of rods (responsible for shape and movement detection) and large cones ensuring nocturnal vision by means of prey movement detection (Mani-Ponset *et al.*, 1993; Sánchez-Vázquez *et al.*, 1995). This ability would facilitate the detection of highly motile prey by this species.

In a laboratory experiment, we investigated the foraging behavior of *D. labrax* post-larvae on *E. affinis* under low light conditions. Then, we assessed the relative vulnerability of the three reproductive stages of *E. affinis* to sea bass larvae in relation to their swimming behavior. Finally, we tested the hypotheses that higher vulnerability of a reproductive stage to predation is due to (i) reduced escape ability, (ii) larger body size and (iii) differential swimming behaviors.

METHOD

Experimental copepods

Eurytemora affinis is a brackish-water egg-carrying copepod that inhabits a wide salinity range (2.5–30) in the Seine estuary (Mouny and Dauvin, 2002; Devreker, 2007). Individuals of this species show a marked sexual

dimorphism (Souissi *et al.*, 2010). Ovigerous females that carry an egg sac are bigger than both males and non-ovigerous females. The size of *E. affinis* in the Seine estuary is characterized by a clear seasonality (Souissi, 2010). During October 2007, the prosome length and width were 846.33 μm (SD = 36.81 μm) and 311.89 μm (SD = 18.17 μm), respectively, whereas those of males were 829.89 μm (SD = 28.74 μm) and 252.66 μm (SD = 13.97 μm), respectively. The mean length of the egg sac was 399.79 μm (SD = 100.16) corresponding to 47.24% of the prosome length of an ovigerous female (Souissi, 2010). Monospecific samples were collected from the Seine estuary, near the Tancarville Bridge during ebb tide in October 2007. Collection was performed using oblique tows of a WP2 net (200 μm). Copepods were brought to the laboratory in ice-boxes filled with aerated water from the sampling site. In the laboratory, adults and late copepodids were sieved (200 μm mesh size) and immediately transferred to a 300 L maintenance tank filled with a mixture of filtered sea water and deionized water at salinity 15. Salinity was thereafter progressively increased to 25 by gradually adding filtered sea water. Salinity 25 was chosen in order to ensure a tradeoff between fish rearing salinity (32) and the copepods maximum distribution salinity range (5–18) in the Seine estuary (Mouny and Dauvin, 2002; Devreker, 2007). Copepods were fed daily on the red alga *Rhodomonas marina* during the 3 days preceding the experiments and water temperature was maintained at 18°C.

Experimental fish

The European sea bass (*D. labrax*) is a commercially important fish species that inhabits both marine and estuarine environments in Europe (Kelly, 1988). Larval stages of this fish start colonizing estuaries of the English Channel, during May–June (Kelly, 1988). Post-larvae, 47 days post-hatching (TL = 19.4 \pm 3 mm) of this species were brought to the Marine Station of Wimereux (France) from the Marine Hatchery of Gravelines (France), which is 50 km far from the laboratory. We selected this developmental stage because we regularly collected similar size individuals during our field sampling for copepods in the Seine estuary. In addition, preliminary experiments showed that smaller larvae were unable to feed on adults of *E. affinis*. After a progressive acclimation at salinity 25, fish larvae were kept in 30 L aquaria at a temperature of 18°C. The chosen light cycle of 16:8 (light:dark) was consistent with the photoperiod observed at our sampling location during spring which corresponds to the arrival of sea bass post-larvae in the English Channel estuaries (Kelly,

1988). Because the efficiency of hatchery-produced fish larvae in capturing live prey can be improved by learning trials (Hughes *et al.*, 1992), fish stocks were fed exclusively on *E. affinis* for 3 days before starting the experiments. Larvae were then kept without food for the 24 h preceding the experiments.

Observation setup

A cubic glass container (15 × 15 × 15 cm; 3.375 L) was used for all observations. In order to record the vertical projection (two-dimensional) of the motion of copepods and fish, we used a single infrared-sensitive camera (DV Sony DCR, 25 Hz) facing one of the four vertical vessel walls.

In turbid estuarine waters, visible light is rapidly attenuated (Kirk, 1979; 1994) and the peak of irradiance is observed at wavelengths above 600 nm (Guthrie and Muntz, 1993). In an attempt to mimic the limited light conditions experienced by both *E. affinis* and *D. labrax* in their natural environment and to prevent copepod phototropism, we performed our experiments under near infrared illumination. Light-emitting diodes (LED, 880 nm) were placed below the experimental vessel and provided the only illumination source.

Experimental procedure

We sorted copepods according to their reproductive stage: males, non-ovigerous females (females hereafter) and ovigerous females. For our experiments, we used a density of 43 ind. L⁻¹ comparable with regularly recorded densities of adult *E. affinis* in the Seine estuary (Devreker, 2007; Devreker *et al.*, 2008). Before each treatment, 145 copepods of the same reproductive stage (males, females or ovigerous females) were transferred into the filming vessel filled with 3.12 L of filtered water and allowed to acclimatize for 15 min. Behavior of the copepods was thereafter recorded for 20 min. Then, three fish larvae were placed in a separate 250 mL beaker and acclimatized for 15 additional minutes. Subsequently, the larvae were gently added into the experimental vessel containing the original copepods and the behavior of the animals was recorded during 30 min. For each prey treatment (males, females and ovigerous females), four replicates were performed yielding, a total of 10 h of video recordings. In total, we used 1740 copepods as prey and 36 fish larvae as predators. The water temperature measured before and after each experiment ranged from 18 to 21°C. The whole experimental sequence is summarized in Table I.

Table I: Summary data of the experimental procedure used to investigate *E. affinis* behavior and vulnerability to predation by *D. labrax* post-larvae.

| | Number of prey | Number of predators | Recording duration (minutes) | Number of replicates |
|-------------------|----------------|---------------------|------------------------------|----------------------|
| Males | 145 | 0 | 20 | 4 |
| Females | 145 | 0 | 20 | 4 |
| Ovigerous females | 145 | 0 | 20 | 4 |
| | | 3 | 30 | |

Video analyses

Predator behavior

We first proceeded to a visual examination of all of the six videos in which predators were present in order to identify and label the following predator behaviors:

- Attack (A), when a predator strikes on a prey;
- Capture (C), when a predator succeeds in engulfing the prey after an attack;
- Rejection (R), when a prey is rejected from the larva's mouth after a successful capture;
- Ingestion (I), when no rejection occurs after a successful capture;

Capture success (CS), which is computed as the percentage of the average number of captures to attacks:

$$CS = \left\langle \frac{C}{A} \right\rangle \times 100 \quad (1)$$

CS values range from 0 to 100% as attack efficiency increases, with high values being associated with prey with less efficient escape responses.

Prey behavior

The vertical projections of the swimming paths of copepods were digitized using the LabTrack software (Labtrack, 2.1, ©Bioras). Swimming paths of more than 10 s of duration and occurring at least 1 cm away from the bottom and from the walls parallel to the camera axis were considered for further analysis. A data base of 2816, 2296 and 2129 trajectories for males, females and ovigerous females, respectively, was obtained. Parameters likely to affect the predator-prey interaction, copepod swimming speed (Blais and Maly, 1993; Kiørboe, 2008) and escape reaction were compared among treatments (reproductive stages in both absence and presence of predators).

SPEED

Instantaneous speeds (V_i) in mm s^{-1} were computed at the lowest time resolution (0.04 s) as follows:

$$V_i = \frac{\sqrt{(x_b - x_a)^2 + (y_b - y_a)^2}}{0.04} \quad (2)$$

where x and y are the horizontal and vertical displacements, respectively, and ‘a’ and ‘b’ two successive frames. To compare the swimming speeds across reproductive stages, we first averaged the instantaneous speeds for each trajectory (V_i) and then computed the mean speed for each reproductive state (V_{rs}).

ESCAPE REACTION

Acceleration is an important attribute of escape behavior for zooplankton prey. Indeed, maximum accelerations are more likely to be observed for smaller particles that need to escape from their larger predators. In a previous study, using high speed cameras (1000 Hz), Buskey *et al.* (Buskey *et al.*, 2002) have recorded acceleration as high as 255 and 319 m s^{-2} for the copepods *Acartia tonsa* and *A. lilljeborgii*, respectively. For the present study, our video recording frequency of 25 Hz is unlikely to have been high enough to resolve the exact copepod acceleration. Rather, we compared escape reactions performed by the different reproductive stages measured at the same temporal scale.

Escape reactions were estimated as the apparent instantaneous accelerations (A_i) as follows:

$$A_i = \frac{|V_{i+1} - V_i|}{0.04} \quad (3)$$

As for velocities, a mean acceleration was computed for each reproductive state (A_{rs}) out of the mean apparent accelerations for each trajectory (A_i). The (A_{rs}) were compared across treatments.

Statistical analyses

Comparisons of ingestions (I), CS and rejections (R) across treatments were made using the χ^2 test following McDonald (McDonald, 2009). Comparisons of the mean swimming speeds (V_{rs}) as well as the escape reactions (A_{rs}) were performed using the non-parametric Kruskal–Wallis (K–W) test. When a difference was detected, the Wilcoxon test was used to compare means pairwise. For pair comparisons, a Bonferroni adjustment was performed. These tests were performed using the

Statistical Toolbox of MatLab® software (7.5, ©The Math Works, inc.).

RESULTS

Sea bass larvae were pause-travel predators altering swimming bouts with pauses during which they detected prey items.

Males, females and ovigerous females of *E. affinis* did not suffer the same mortality (Table II; Fig. 1; χ^2 , $P < 0.01$). Ovigerous females suffered 75 and 63% higher mortality than males and females, respectively. Females experienced 32% higher predation than males. However, this difference was not statistically significant (χ^2 , $P > 0.05$).

Table II: Summary data of *D. labrax* post-larvae predatory behavior on each of the reproductive stages of *E. affinis*.

| | Males | Females | Ovigerous females |
|----------------------|-------|---------|-------------------|
| Number of attacks | | | |
| Mean | 17.8 | 23.8 | 63.3 |
| s.e. | 9.7 | 8.3 | 26.9 |
| Number of captures | | | |
| Mean | 10.0 | 15.0 | 42.0 |
| s.e. | 5.7 | 8.6 | 18.6 |
| Number of rejections | | | |
| Mean | 0.0 | 0.3 | 1.5 |
| s.e. | 0.0 | 0.3 | 0.6 |

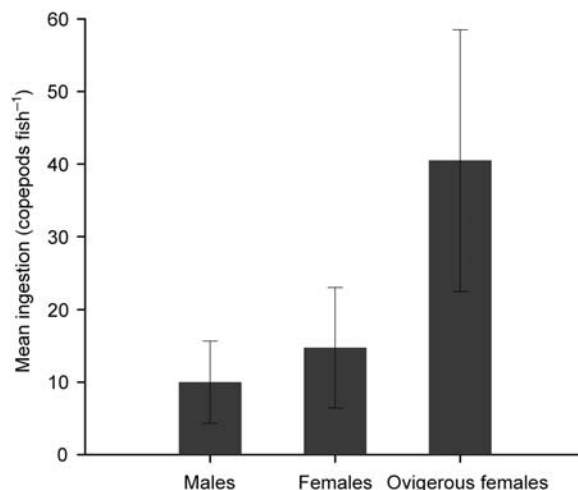


Fig. 1. Mean (\pm s.e.) number of males, females and ovigerous females of the copepod *E. affinis* ingested per *D. labrax* larva.

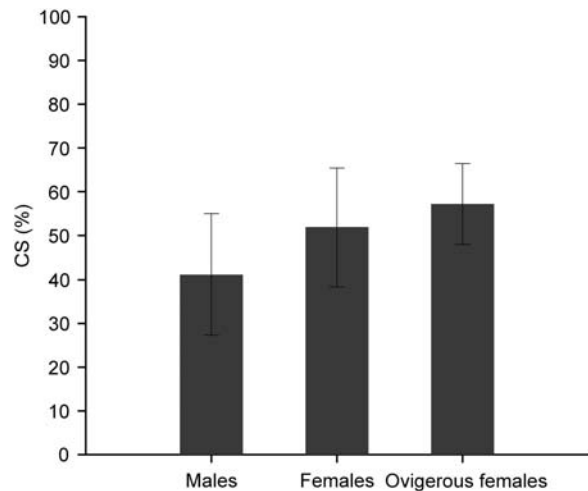


Fig. 2. CS of *D. labrax* larvae on males, females and ovigerous females of the copepod *E. affinis* (mean \pm s.e.).

No significant differences were detected in CS across the treatments (Fig. 2; χ^2 , $P > 0.05$). Likewise, rejections, which represented only 2.7% of the overall attacks (Table II), were not significantly different among the prey treatments (χ^2 , $P > 0.05$).

Prey behavior of the different reproductive stages

In the absence of predators

There were significant differences in the mean swimming speeds (V_{rs}) and escape reactions (A_{rs}) among reproductive stages (Figs 3 and 4; K–W, $P < 0.001$). Mean speeds (V_{rs}) as well as mean escape reactions (A_{rs}) were not significantly different between males and ovigerous females (Figs 3 and 4; Wilcoxon, $P > 0.05$). However, females had significantly lower mean speeds and escape reactions than both males and females (Figs 3 and 4; Wilcoxon, $P < 0.001$).

In the presence of predators

Mean swimming speeds (V_{rs}) were significantly different across reproductive stages (K–W, $P < 0.001$). Ovigerous females swam faster than males (Wilcoxon, $0.05 < P < 0.01$), which in turn swam faster than females (Fig. 3; Wilcoxon, $P < 0.01$). This trend was corroborated by the Probability Density Function (PDF) distribution of instantaneous speeds (Fig. 5). The different reproductive stages of the copepod *E. affinis* displayed different escape reactions (Fig. 4; K–W, $P < 0.001$). No differences could be detected between the escape reactions of males (Fig. 4;

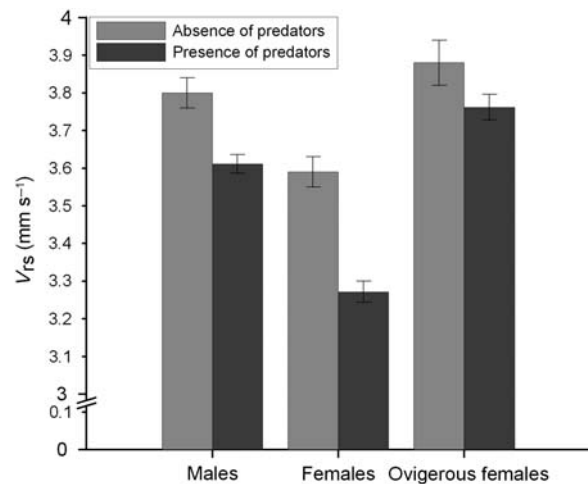


Fig. 3. Mean speed (V_{rs}) (\pm s.e.) for males, females and ovigerous females of the copepod *E. affinis* in both the absence and presence of predators ($N = 7241$).

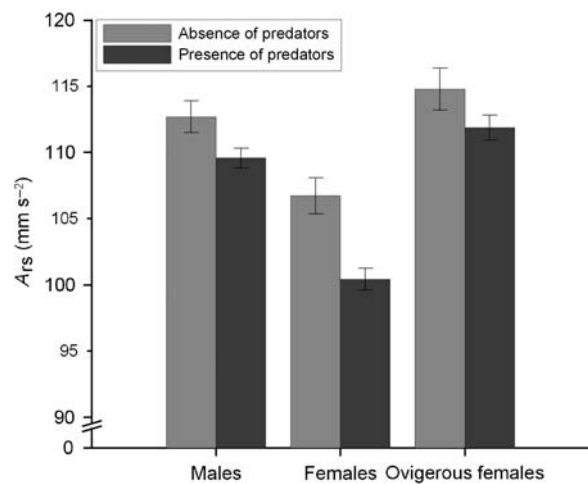


Fig. 4. Escape reactions (A_{rs}) for males, females and ovigerous females of the copepod *E. affinis* in both the absence and presence of predators ($N = 7241$).

$109.5 \pm 34.6 \text{ mm s}^{-2}$) and ovigerous females (Fig. 4; $111.8 \pm 38.7 \text{ mm s}^{-2}$; Wilcoxon, $P > 0.05$). However, females had a significantly lower escape reaction (Fig. 4; $100.4 \pm 33.2 \text{ mm s}^{-2}$) than both males (Wilcoxon, $P < 0.001$) and ovigerous females (Wilcoxon, $P < 0.001$). The same trend was observed in the PDF of the escape reactions (Fig. 6).

Prey behavior in the absence versus presence of predators

The mean swimming speed of both males and females significantly decreased when predators were present

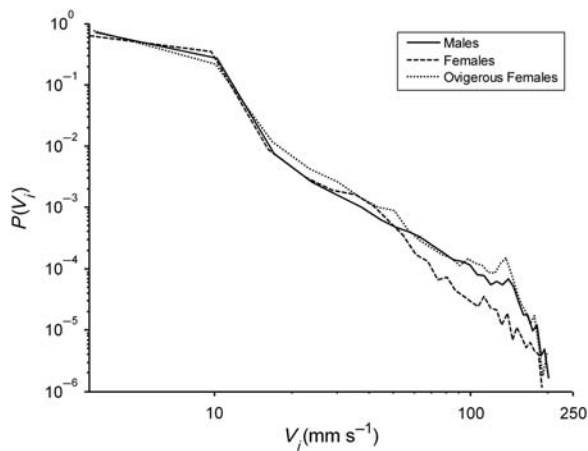


Fig. 5. PDF of the instantaneous speeds (V_i) for males, females and ovigerous females of the copepod *E. affinis* in the presence of predators ($N = 5.2 \times 10^6$).

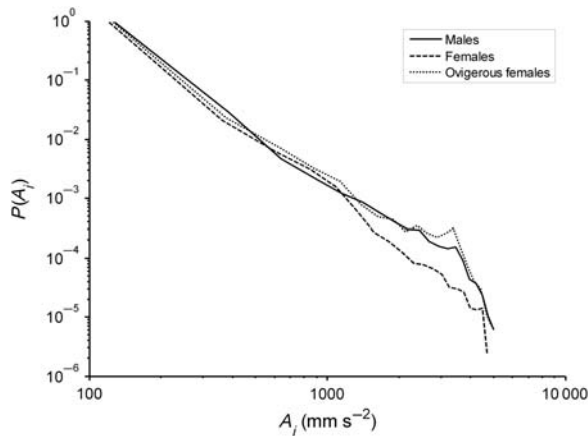


Fig. 6. PDF of the escape reactions (A_i) for males, females and ovigerous females of the copepod *E. affinis* in the presence of predators ($N = 5.2 \times 10^6$).

(Fig. 3; Wilcoxon, $P < 0.001$). However, the presence of predators did not significantly affect the mean speed of ovigerous females. The same trend was observed for escape reactions, with a significant decrease for males and females (Fig. 4; Wilcoxon, $P < 0.001$) and no significant change for ovigerous females (Fig. 4; Wilcoxon, $P > 0.05$).

DISCUSSION

Larval behavior

Our observations showed that *D. labrax* larvae are pause-travel predators corroborating the results of Georgalas *et al.* (Georgalas *et al.*, 2007). This is a strategy

adopted by species inhabiting environments with “heterogeneous background” (e.g. estuaries) intended to facilitate the detection of moving prey (Janssen, 1982).

Differential vulnerability of *E. affinis* reproductive stages

Higher vulnerability of ovigerous females has already been reported for *Euchaeta elongata* (Bollens and Frost, 1991), *Eudiptomus gracilis* (Svensson, 1992; Svensson, 1997a,b; Nassal *et al.*, 1998) and *Eurytemora* spp. (Sandstorm, 1980; Vuorinen *et al.*, 1983). Our experimental data corroborated these results and showed that *E. affinis* ovigerous females were more vulnerable to their natural predator from the Seine estuary than the other reproductive stages. Here, we discuss three hypotheses that account for the enhanced vulnerability of ovigerous *E. affinis* to predators.

Hypothesis 1: Higher vulnerability of ovigerous females to predators is due to reduced escape ability

The successive events occurring during a successful predation sequence are: the encounter, the pursuit, the attack, the capture and the ingestion. It has been argued that the enhanced drag, due to the presence of the egg sac, is responsible for less efficient escape responses of ovigerous females during pursuit or attack events (Winfield and Townsend, 1983; Svensson, 1992, 1997a). However, this study revealed that ovigerous female *E. affinis* are capable of more vigorous escape reactions than either males or females in both the absence and presence of predators. Moreover, the capture success of *D. labrax* post-larvae was not significantly different across *E. affinis* reproductive stages. In other words, all reproductive stages are equally susceptible to being captured once attacked. The higher mortality of ovigerous females seems therefore to be governed by events occurring either downstream of the capture (i.e. rejection) or upstream of the pursuit. The numbers of rejections were similar among treatments, the higher vulnerability of ovigerous females should therefore be attributed to events occurring before the pursuit. We accordingly reject the first hypothesis and assume that the observed differential mortality is not due to different escape abilities.

Hypothesis 2: Higher vulnerability of ovigerous females to predators is due to their larger body size

As documented for *E. gracilis* (Svensson, 1997b), higher vulnerability of ovigerous females can be explained by their larger size. In fact, it has already been shown that bigger prey are detected at farther distances from the predator than smaller prey (O’Brien, 1987). If size alone

accounts for higher ingestion rates, then one would expect ovigerous females to suffer higher mortality than males, which in turn would experience higher mortality than males. However, as reported for *Eurytemora hirundoides* (Vuorinen *et al.*, 1983), our results show no mortality difference between males and females of *E. affinis*. Though size alone does not explain the observed differential mortality, it may act in synergy with another parameter. In fact, Kiørboe and Visser (1999) theoretically demonstrated that, in predators, perception is dependent on both prey size and velocity (Kiørboe and Visser, 1999). Therefore, our second hypothesis is neither rejected nor completely accepted.

Hypothesis 3: Higher vulnerability of ovigerous females to predators is due to differential swimming behavior

Larval fish may perceive the swimming patterns of prey both qualitatively and quantitatively. In estuarine areas with high densities of non-living suspended matter, prey movement patterns can be used to discriminate living prey from inert particles (Buskey *et al.*, 1993). Moreover, a predator detects a moving prey at farther distances than a stationary one (Wright and O'Brien, 1982). Similarly, an increased swimming activity of prey usually results in higher vulnerability to larval fish predators (Sullivan *et al.*, 1983; Petersen and Ausbel, 1984; Meng and Orsi, 1991). The behavior of the copepod may therefore be one of the major determinants responsible for the observed differential vulnerability. In this study, two behavioral parameters differed among adult reproductive stages: the swimming speed and the escape reaction (i.e. apparent acceleration). Swimming speed of a prey is known to trigger sensory perception in planktivorous predators (Buskey *et al.*, 1993; Kiørboe, 2008). However, acceleration is unlikely to be perceived by larval fish because a relatively large body (i.e. fish larvae) cannot be embedded in the flow generated by a small planktonic prey (Kiørboe and Visser, 1999; Kiørboe, 2008). In our study, males and females had slightly higher mean speed and escape reaction in the absence of predators. This reduction in activity may be explained as an anti-predator behavior intended to decrease conspicuousness and encounter rates. In fact, increased speed generates a stronger hydromechanical signal (Tiselius and Jonsson, 1990), which can be perceived from longer distances (Kiørboe and Visser, 1999). In addition, a fast moving prey is exposed to higher encounter rates with predators (Gerritsen and Strickler, 1977). On the other hand, ovigerous females did not significantly decrease their swimming activity. It is therefore reasonable to attribute the higher vulnerability of ovigerous females to their stronger hydro-mechanical disturbance and their higher encounter

rates with predators. The last hypothesis can therefore be maintained.

Generalization

In a general predator–prey encounter framework, the ovigerous females that are bigger and swim faster produce stronger hydromechanical disturbance and are more likely to be encountered by larval fish than slower prey (i.e. males and females). They consequently suffer higher mortality than males and females. Conversely, the females that swim slower than males produce a moderate hydromechanical disturbance and have lower contact rates with predators, which compensates for their larger size. Accordingly, no mortality differences could be observed between males and females. From a mechanistic perspective, our study corroborates theoretical results demonstrating that physical contact rates, i.e. the presence of a prey in the perceptive field of a predator, are not necessarily equivalent to encounter rates. In fact, as highlighted by Visser (Visser, 2001), prey swimming speed is also important for predator–prey encounters. We therefore emphasize the need to take into account the role of prey behavior as a key factor governing prey conspicuousness to predators when modeling predator–prey encounters in the plankton.

Ecological implications

If the higher swimming activity of *E. affinis* ovigerous females puts them at disadvantage, it may be questioned how *E. affinis* remains a dominant copepod species in the Seine estuary and why this behavior has not been selected against? One first explanation could be drawn from the results of Svensson (Svensson, 1996) who observed frequent viable egg detachment in the copepod *Eudiptomus gracilis* after being attacked by a predator. This author suggested that this behavior may be advantageous to overcome the drawbacks of the higher vulnerability of ovigerous females (Svensson, 1996). However, in our experiments we did not observe any clutch detachment in ovigerous females of *E. affinis*. Rather, we suggest that higher predation on ovigerous females of *E. affinis* might not necessarily impair their reproductive success. In fact, several studies revealed that eggs of various copepod species (Redden and Daborn, 1991; Conway *et al.*, 1994; Saint-Jean and Pagano, 1995; Bartholme *et al.*, 2005) including *E. affinis* (Conway *et al.*, 1994; Flinkman *et al.*, 1994) can remain viable following ingestion and passage through the gut of planktivorous fishes. Both Redden and Daborn (Redden and Daborn, 1991) and Flinkman *et al.*

(Flinkman *et al.*, 1994) suggested that this adaptation prevents egg-carrying copepods from the disadvantages of enhanced predation against their ovigerous females. In the Seine estuary, adult *E. affinis* were found over a wide range of salinities (from 5 to 15) in May 2004 (Devreker *et al.*, 2008). However, high nauplii densities were only observed in the low salinity zone (from 0 to 5), which is consistent with their optimal salinity for faster development (Devreker *et al.*, 2004). Devreker *et al.* (Devreker *et al.*, 2008) attributed this distribution discrepancy to differential swimming abilities of the different developmental stages. The rationale is that, contrary to nauplii that are aggregated as passive particles, adults are capable of tidal-governed vertical migrations (Morgan *et al.*, 1997) and can spread over wider areas (Devreker *et al.*, 2008). Fish larvae are also able to perform tidal vertical migrations in order to maintain their upstream position in estuaries (Fortier and Legget, 1983). Here, we suggest that *D. labrax* post-larvae, which colonize the English Channel estuaries during May and June (Kelly, 1988), may also facilitate *E. affinis* nauplii dispersal. In order to validate this hypothesis, further experiments should assess the presence of viable subitaneous copepod eggs in the feces of *in situ*-collected ichthyoplankton.

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