

## Multifractal anisotropic swimming: the optimal foraging behaviour of grouper larvae

M. S. MAHJOUB\*<sup>†</sup>, G. DUR<sup>†</sup><sub>‡</sub>, S. SOUISSI\*, F.G. SCHMITT\* AND J.S. HWANG<sup>†</sup>

\*Univ. Lille, CNRS, Univ. Littoral Cote d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences, F 62 126 Wimereux, France and <sup>†</sup>Institute of Marine Biology, National Taiwan Ocean University, 202 Keelung, Taiwan

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It was hypothesized that the Malabar grouper *Ephinephelus malabaricus* larvae have developed search patterns adapted to the distribution of their prey to maximise their net energy intake per unit time. Analysis of the swimming behaviour of *E. malabaricus* larvae in both the presence and absence of *Artemia* sp. nauplii is presented to test this hypothesis. A method derived from turbulence studies (the moment function of the displacements) was used to characterize the behaviour. The results revealed that larval swimming pattern was multifractal (intermittent and long-range-correlated) and isotropic (*i.e.* uniform in all directions) in the presence of prey, but multifractal and anisotropic (*i.e.* more frequent long displacement on the vertical axis) in the absence of prey. It is suggested that the search behaviour observed in the absence of prey is an adaptive response to prey distribution pattern, which is often characterised by multifractality and anisotropy (*i.e.* larger patches on the horizontal axes). In the presence of prey, *E. malabaricus* shifted to intensive search behaviour. Other possible contributors to the observed patterns are discussed. It is concluded that multifractality and anisotropy of swimming patterns observed in the experiment are mainly explained in an optimal foraging theory framework.

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### INTRODUCTION

Predator–prey encounters in the plankton have been a challenging topic for marine ecologists since Gerritsen & Strickler (1977) first modelled the encounter probabilities in the zooplankton. At the individual scale, encounters depend on motion which, in the absence of strong turbulence, is inherent to the motility of the planktonic organisms (Kiørboe, 2008; Michalec *et al.*, 2015). In the aquatic realm, where prey distribution is patchy, finding high-density food areas is essential for predators (Lasker, 1975; Eldridge *et al.*, 1982; Lasker & Zweifel, 1987; Mohammadian *et al.*, 1997), especially when prey densities outside patches are below the growth-threshold (Peck & Daewel, 2007). According to the optimal foraging theory, a predator should adopt a foraging behaviour that maximizes its net energy intake per unit time (MacArthur & Pianka, 1966; Stephens & Krebs, 1986). In addition, theoretical evidence shows that optimal foraging behaviour should be different when searching for and within patches

<sup>‡</sup>Author to whom correspondence should be addressed. Tel.: +33 32 199 2937; email: gael.dur@univ-lille1.fr

(Reynolds, 2012). Several zooplanktonic groups including fish larvae are able to adjust their swimming behaviour to the distribution of their prey in order to maximize encounters (Munk & Kjørboe, 1985; Coughlin *et al.*, 1992).

There is a large body of literature addressing optimal search strategies for predators (Pitchford *et al.*, 2003; Sims *et al.*, 2008; Alpern *et al.*, 2011). Various empirical studies claim that marine organisms as diverse as dinoflagellates (Bartumeus *et al.*, 2005), turtles and sharks perform foraging behaviours that can be described by a Lévy distribution (Sims *et al.*, 2008). Lévy walks (LW) have been advocated to increase foraging success in environments with randomly distributed patches (Bartumeus *et al.*, 2005; Sims *et al.*, 2008). Plankton prey patch distribution, however, is often multifractal (*i.e.* intermittent and long-range-correlated) due to its coupling with turbulence (Pascual *et al.*, 1995; Seuront & Lagadeuc, 2001). In addition, plankton patches are often reported to be anisotropic (*i.e.* directionally dependent) (Gallager *et al.*, 2004). As a result, search strategies of planktonic predators to have evolved would be expected accordingly.

Analysing the motion patterns of predators could give insight into their foraging strategy and test the above hypothesis. In animal behaviour, however, intermittency is a commonly observed feature (Reynolds, 2006) as it maximizes foraging efficiency (Bénichou *et al.*, 2011). This is particularly true when observing the movements of planktonic organisms, whose behaviours are typically intermittent (Hwang *et al.*, 1994; Schmitt & Seuront, 2001; Titelman & Kiorboe, 2003; Schmitt *et al.*, 2006; Alcaraz *et al.*, 2007). Such intermittency leads to high intra-individual variance levels. In addition, behaviour of foragers may exhibit a multi-scale complexity rendering their analysis challenging (Gautestad, 2012). In order to thoroughly interpret such data, using the moment function of the displacement, initially developed for the study of intermittent phenomena in fluid dynamics (*i.e.* turbulence) is suggested. This method allows the differentiation of different walk types (Fig. 1) that include: (1) Brownian motion (BM), which is characterized by a large number of short displacements and very few long displacements, and (2) anomalous diffusion for which long displacements are more frequent than in the Brownian case. Among anomalous diffusion, two additional walk types are distinguished: (3) multifractal random walks (MRW) which have the highest frequency of long displacements (Bacry *et al.*, 2001; Schmitt & Seuront, 2001) from (4) Lévy walks (LW) which have groups of short displacements separated by longer displacements (Reynolds, 2012). Here the method of moment function of the displacement is applied to the swimming behaviour of Malabar grouper *Epinephelus malabaricus* (Bloch & Schneider 1801) larvae in both the absence and presence of planktonic prey, *i.e.* *Artemia* sp. nauplii. The objective was to test the hypothesis that grouper larvae exhibit a multifractal and anisotropic foraging behaviour depending on prey availability.

## MATERIAL AND METHODS

The experimental procedure was the same as in Mahjoub *et al.* (2011). The swimming behaviour of four *E. malabaricus* larvae (25 days old; mean  $\pm$  s.d.  $7.1 \pm 1.0$  mm total length) was recorded in triplicate in the absence and then presence of 100 freshly hatched *Artemia* sp. nauplii (prey) in calm water conditions. The number of *E. malabaricus* larvae in the vessel was based on grouper *Epinephelus suillus* (Hamilton 1822) larvae rearing protocols recommending densities of 5 individuals  $l^{-1}$  (Duray *et al.*, 1997). Prey were gently added using a pipette and

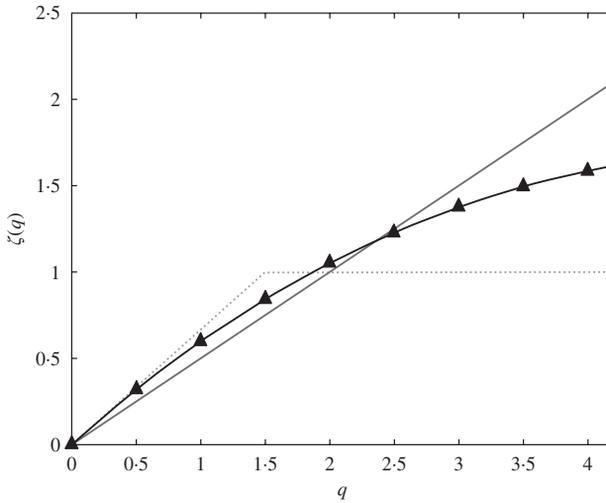


FIG. 1. Typical moment functions  $\zeta(q)$  for several cases: Brownian motion (BM, —), Lévy walk (LW) with  $\alpha = 1.5$  (.....) and a multifractal random walk (MRW, ▲) with a non-linear moment function. Modified from Schmitt & Huang (2016).

were left in the presence of their predator for an acclimation period of 10 min before recording. This time allowed for the water flow to stabilise. Larvae behaviour was recorded during the night for 20 min in a 11 (10 × 10 × 11 cm) glass experimental tank (salinity: 25; temperature: 27° C, range ± 1° C) using two HDD cameras (Sony SR100, 30Hz; www.sony.com). The size of the vessel provided enough space for the *E. malabaricus* larvae to prey freely and allow the entire tank to be in the field of view. Cameras were placed facing two orthogonal sides in order to reconstruct three-dimensional (3D) trajectories. Light was provided by a 9 W lamp (120 V, 60 Hz) suspended 45 cm above the experimental tank. *Ephinephelus malabaricus* larvae paths were manually tracked using the TrackIt (Net Tech Consulting, Iguana Gurus; www.net-tech.us) software. To avoid sidewall effects, behaviours occurring less than one body length away from the tank walls were discarded. Each digitized path was recorded as a matrix of the spatial co-ordinates of the larva over time ( $X, Y, Z, t$ ) with  $X, Z$  and  $Y$  being the two horizontal and the vertical axes, respectively. For each condition, several trajectories were extracted with a total of 11 and nine trajectories in the absence and presence of prey, respectively. The average durations of analysed trajectories were (mean ± s.d.)  $38.6 \pm 19.6$  s in the absence of prey and  $35.7 \pm 18.8$  s in presence of prey. These trajectories represent a total of 22 388 data points with 12 740 points in the absence of prey and 9648 points in the presence of prey.

Calculations of the moment function of the displacements are explained in what follows. If  $\Delta X_\tau$  is considered to be the displacement of a planktonic organism in one dimension during the time increment  $\tau$

$$\Delta X_\tau = X(t + \tau) - X(t) \quad (1)$$

The norm of this displacement in 3D is:

$$\|\Delta X_\tau\| = [(X(t + \tau) - X(t))^2 + (Y(t + \tau) - Y(t))^2 + (Z(t + \tau) - Z(t))^2]^{1/2} \quad (2)$$

For processes with stationary increments, the moments of order  $q$  ( $q > 0$ ) of this norm are only dependent on the time step  $\tau$ . For scaling processes, the statistical mean of the moments of order  $q$  can thus be written as:

$$\langle \|\Delta X_\tau\|^q \rangle \propto \tau^{\zeta(q)} \quad (3)$$

where  $\zeta(q)$  is the scale-invariant moment function that characterizes the complexity of the lagrangian paths (Schmitt & Seuront, 2001). The slope of the power fit of the log-log plot of  $\langle ||\Delta X_\tau||^q \rangle > v \cdot \tau$  for each  $q$  value provides  $\zeta(q)$ . The appropriate range of scales  $\tau$  on which the exponent  $\zeta(q)$  was estimated was chosen according to the 'R<sup>2</sup>-SSR' criterion (Seuront *et al.*, 2004a). Briefly, a regression window of varying width was considered ranging from a minimum of 10 data points (to ensure statistical relevance of the regression analysis) to the entire data set. The windows were slid along the entire data set at the smallest available increments, with the whole procedure iterated  $n-9$  times, with  $n$  the total number of available data points. Within each window and for each width, the coefficient of determination ( $r^2$ ) and the sum of the squared residuals for the regression were estimated. The values of  $\tau$  (equation 3) and  $\zeta(q)$  were subsequently used, which maximized the coefficient of determination and minimized the total sum of the squared residuals to define the scaling range and estimate  $\zeta(q)$ .

Calculations were made using a custom programme implemented in MatLab (7.5, The Math Works, Inc.; www.mathworks.com) used in Dur *et al.* (2010). When  $\zeta(q) = q/2$  the path has the properties of a normal (Brownian) motion for which displacements are normally distributed variables. When  $\zeta(q) \neq q/2$  the walk belongs to anomalous diffusion. The Lévy walk is the case where:

$$\zeta(q) = \frac{3 - \alpha}{2}q \quad (4)$$

where  $\alpha$  is the Lévy walk index ( $0 < \alpha < 2$ ) (Schmitt *et al.*, 1999). If  $\zeta(q)$  is non-linear across the moments  $q$ , then the walk is said to be multifractal.

## RESULTS

In both conditions the larvae moved actively in fluctuating and irregular ways, alternating between periods of relatively straight and smooth swimming and periods of more erratic motions. Space utilisation was nevertheless different depending on prey availability. In the absence of prey, the larvae presented long vertical displacements ensuring higher space occupation in the vertical axis (Fig. 2). When prey were present, larvae swam in smaller volumes and did not exhibit any preference for either the horizontal or vertical plane within that search volume (Fig. 2).

The properties of the tracks in the 3D space and the three 2D projections in the  $xy$ ,  $xz$  and  $yz$  planes were considered. This is of prime interest to investigate potential differential behaviour on the vertical and horizontal views (anisotropy).

The analysis of the displacements revealed a very good scaling for a range over a decade in both conditions (Fig. 3). The statistics (optimum scaling range and coefficient of determination) of the power fit of the log-log plot of  $\langle ||\Delta X_\tau||^q \rangle > v \cdot \tau$  for the 3D, the vertical projection XY, the vertical projection ZY and the horizontal projection XZ are provided in Fig. 4. For moments up to  $q = 4$ , the coefficient of determination was always  $>0.99$  confirming the appropriateness of the moment range used for the fits. More specifically, the scaling manifested for time scales ranging from 0.07 to 5 s for both the 3D and 2D projections in presence of prey. In the absence of prey, the scaling manifested for time scales ranging from 0.07 to 2 s for the horizontal plane, and from 0.07 to 7 s for the vertical planes and the 3D projection. Considering the average speed in the presence and absence of prey (7 and 8.5 mm s<sup>-1</sup>), the amplitude of displacements structured in a scale-dependent (*i.e.* scaling) way can be defined. This amplitude is bounded for distances between 0.5 and 45 mm in the presence of prey. In the absence of prey displacements between 0.6 and 60 mm are structured in a scale-dependent way. This stressed that the departure from scaling for long time scales is different between

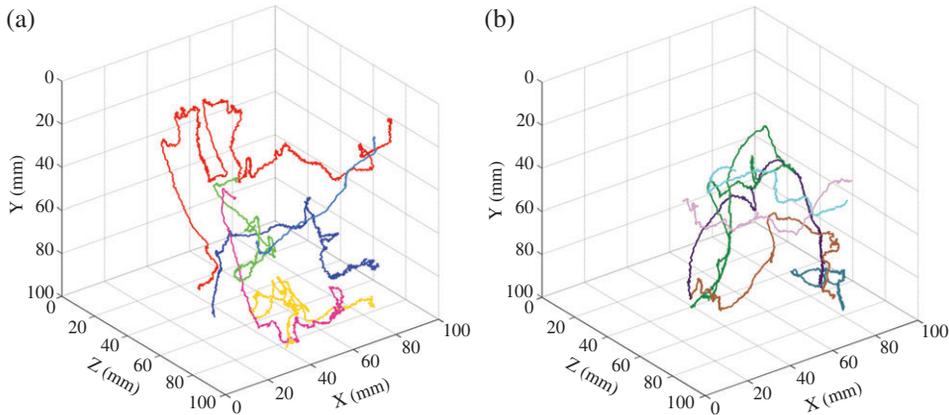


FIG. 2. Examples of three-dimensional (3D) swimming paths of *Ephinephelus malabaricus* larvae recorded at 30 Hz in the (a) absence of prey and (b) presence of prey. Only six representative swimming paths were plotted (one colour per trajectory), although analyses were conducted on nine and 11 trajectories, respectively.

the prey conditions and the horizontal and vertical planes in the condition where prey were absent. These discrepancies between conditions and planes are confirmed below by analysis of the exponent function,  $\zeta(q)$ .

In the present experiment, the obtained  $\zeta(q)$  function, compared to the linear behaviour expected in the case of Brownian motion (*i.e.*  $\zeta(q) = q/2$ ), was non-linear and convex for both prey conditions and for all projections. This revealed the multifractal nature of *E. malabaricus* larvae paths (Fig. 5). In spite of the uniformity of the walk type, there were differences in the scaling of  $\zeta(q)$  depending on prey availability (Fig. 5). In fact, the curvatures of the  $\zeta(q)$  function markedly differed for the two conditions, it was more pronounced in the absence of prey (Fig. 5). This indicates that intermittency was stronger and long displacements were more frequent in the absence of prey.

## DISCUSSION

Empirical determination of walk types could be misleading and the complexity of an organism's behaviour can also lead to wrong categorization of the walk type depending on their prey field (Edwards *et al.*, 2007; Gautestad, 2013; Lundy *et al.*, 2013). Furthermore, composite types of walks could mimic LW (Benhamou, 2007; Plank & James, 2008). In an attempt to avoid errors likely to occur when differential resource availability induces behavioural changes, the foraging behaviour of *E. malabaricus* larvae under different prey conditions was investigated separately.

The former fractal analysis already suggested the existence of anisotropy in the swimming behaviour of *E. malabaricus* (Mahjoub *et al.*, 2011) but it did not show an obvious difference among prey availability conditions. This could be associated with the fact that fractal analysis provided a general vision of the heterogeneity. The multifractal approach is an extension of the fractal approach. These approaches can be compared following the relation  $D = d + 1 - \zeta(2)/2$ , where  $D$  is the fractal dimension,  $d$  is the

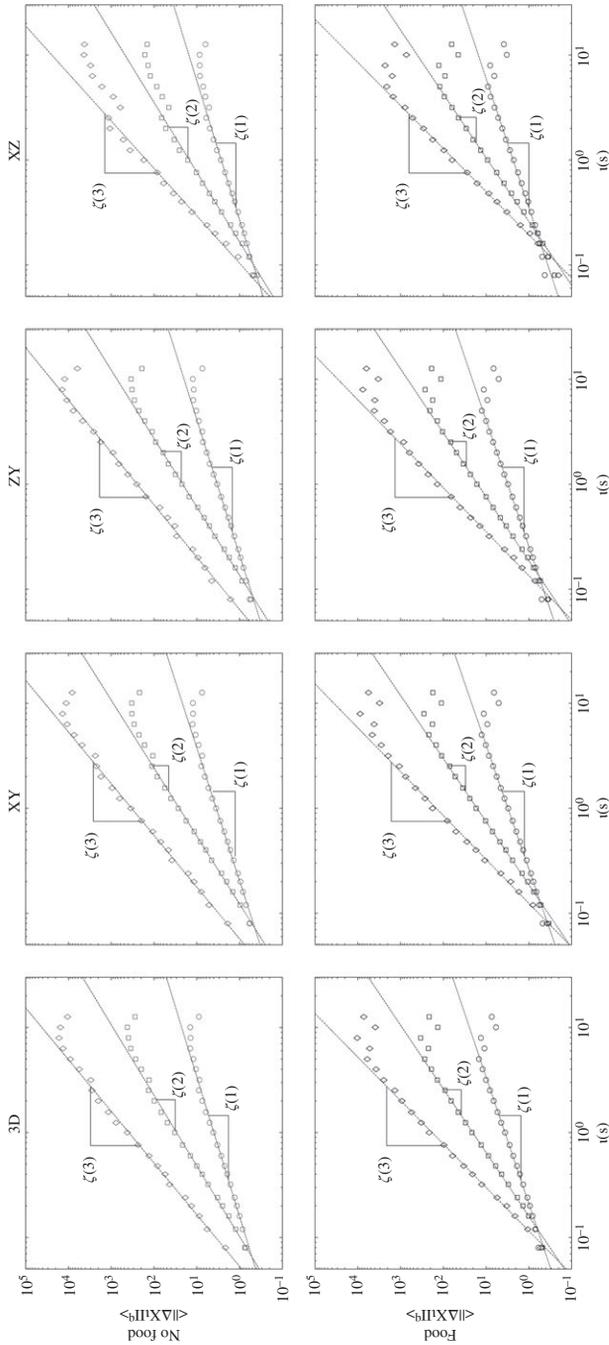


FIG. 3. Moment,  $\langle \|\Delta X_t\|^q \rangle > v$ .  $\tau$  for  $q = 1, 2$  and  $3$  in log-log plots, computed from the swimming paths of *Ephinephelus malabaricus* larvae in three-dimensions (3D), on the vertical projections XY and ZY, and on the horizontal projection XZ, in food (bottom) and no food (top) conditions. The scaling of the moments is good over a decade, ranging from 0.1 to 2 s.

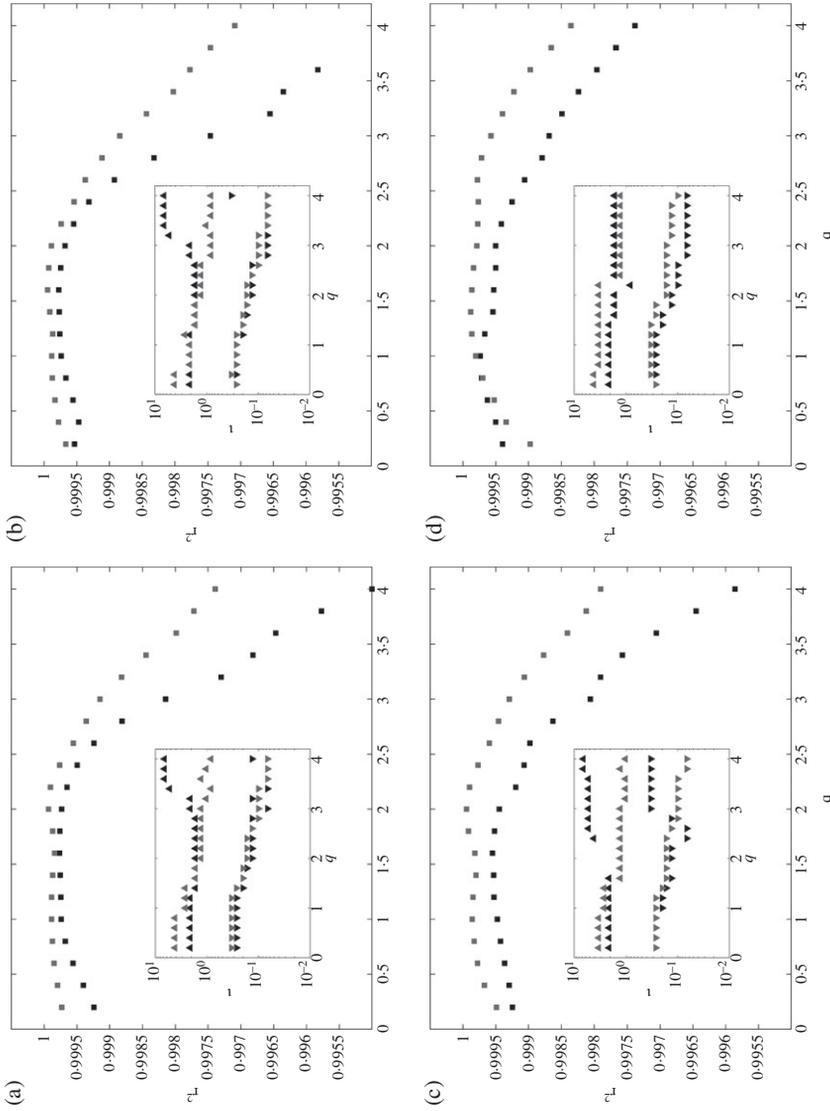


FIG. 4. Statistics ( $\tau^2$ ) of the power fit of the log-log plot of  $\|\Delta X_\tau\|^q > v \cdot \tau$  for (a) 3D, (b) the vertical projection XY, (c) the vertical projection ZY and (d) the horizontal projection XZ. The ranges of scales  $\tau$  used for each fitting are presented in the insert ( $\tau_{\min}$   $\blacktriangledown$ ;  $\tau_{\max}$   $\blacktriangle$ ). Both present the results in the absence of prey ( $\blacksquare$ ) and the presence of prey ( $\blacksquare$ ).

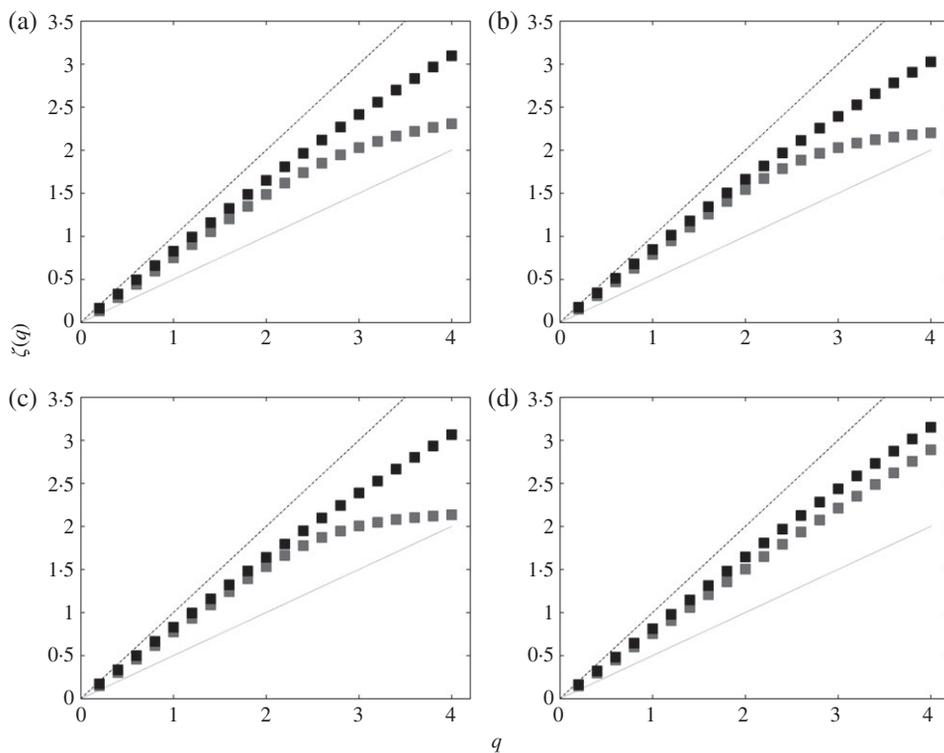


FIG. 5. Scaling of moment function  $\zeta(q)$  for the displacements of *Ephinephelus malabaricus* larvae in (a) three-dimensions (3D), (b) on the vertical projection XY, (c) on the vertical projection ZY and (d) the horizontal projection XZ in the absence (■) and presence (▒) of food. The functions  $\zeta(q) = q/2$  (Brownian motion, —) and  $\zeta(q) = q$  (linear motion, ..... ) are also shown for comparison.

embedding Euclidean space, and  $\zeta(2)$  is a specific value of the multifractal structure function exponents,  $\zeta(q)$  (Seuront *et al.*, 2004a). Multifractal analysis used in the present study, as a generalization of the fractal approach, provided more information on the intermittency and strong fluctuations of the moves. By considering, the whole range of swimming velocities, using a single function, it helped the comparison between the different situations and confirmed the anisotropic behaviour of *E. malabaricus*.

The paths of *E. malabaricus* larvae were multifractal for both prey conditions. This implies that the successive steps of the swimming larvae were not random but long-range-correlated (*i.e.* existence of memory) and that large displacements were more frequent than that observed in a random walk. In the natural environment, planktonic prey patches are characterized by a multifractal (non-random) distribution pattern (Pascual *et al.*, 1995; Seuront & Lagadeuc, 2001). When first addressing the multifractal distribution of zooplankters, Pascual *et al.* (1995) highlighted the lack of knowledge on the underlying mechanisms leading to this pattern. In a general framework, where predators optimize their search activity by adjusting it to the distribution pattern of their prey (Bartumeus *et al.*, 2003; Sims *et al.*, 2008), it is speculated that the multifractal properties of displacements reported from various zooplankters like *Daphnia pluricaria* (Seuront *et al.*, 2004b), copepods

(Schmitt & Seuront, 2002; Dur *et al.*, 2010; Michalec *et al.*, 2013) and *E. malabaricus* larvae (this work), in addition to turbulence, are among the main driving forces that lead to multifractal distribution patterns of plankton in the natural environment.

The observed differences in the scaling of  $\zeta(q)$  depending on prey availability indicate that intermittency was stronger and long displacements were more frequent in the absence of prey, which is consistent with extensive search behaviours. An enhancement of the amplitude of the displacements has been reported for the planktonic copepod *Pseudocalanus elongatus* in the absence of food, and was assumed to increase the chances of encountering a food patch (Kiørboe, 2008). When prey was present, long displacements of *E. malabaricus* were less frequent, revealing a shift to an intensive search behaviour oriented towards smaller volumes. In a theoretical study investigating the effect of motion complexity on encounter rates, Cianelli *et al.* (2009) found no optimal search complexity level in a patchy prey environment. Nevertheless, Pitchford *et al.* (2003) revealed that, in patchy environments, it is more advantageous to remain within the prey aggregation. The observed strategy is intended to keep the predator inside food patches as previously reported for krill *Thysanoessa raschii* (Price, 1989) and *Pleuronectes platessa* L. 1759 larvae (Hill *et al.*, 2002). Area-restricted search is an effective tactic for exploiting prey within patches. It would be inefficient when searching for widely dispersed individuals or patches of prey. This suggested that the less frequent long displacements observed in food condition were associated with the dispersed distribution of *Artemia* sp. patches in the tank. A series of successful strikes will deplete the food in the vicinity of the larvae and there will be no advantage in searching nearby. A long displacement is therefore needed to search a different area. This type of behaviour is described as 'win-shift' behaviour (Hill *et al.*, 2002). The multifractal random walk (MRW) observed here is different from the optimal LW predicted for predators searching for randomly distributed prey patches (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005).

Prey availability affected the directionality of the MRW for *E. malabaricus* larvae. When food was absent, a clear anisotropy characterized by more frequent long displacements on the vertical axis than on the horizontal axis was observed. Several planktonic organisms have been reported to exhibit differential behaviours on the vertical and horizontal views (anisotropy) (Seuront *et al.*, 2004a). In *Daphnia pulex*, such differences in the swimming pattern were mainly attributed to the effects of gravity, and the hop-and-sink swimming behaviour (Seuront *et al.*, 2004a). Here, anisotropy was only observed in the absence of prey. It is suggested that the anisotropic search behaviour of *E. malabaricus* larvae, with long vertical movements, is an adaptation to the horizontal distribution of food patches in the natural environment. In fact, prey fields are usually reported to be horizontally distributed (Haury & Wiebe, 1982; Gallager *et al.*, 2004) which makes an increased motility towards the vertical axis more beneficial in terms of encounters with prey (Jenkins, 1988).

During ontogeny, fish larvae exhibit morphological (Russo *et al.*, 2009), habitat (Frédérich *et al.*, 2012) and diet (Anneville *et al.*, 2011) shifts. Russo *et al.* (2009) have indicated that the sequence of morphological changes during the pelagic life of dusky grouper *Epinephelus marginatus* (Lowe 1834) larvae favours a wait and catch (ambush) rather than a continuous swimming (cruising) feeding strategy. The observed reduction in long displacements for *E. malabaricus* in presence of prey is in agreement with the findings of Russo *et al.* (2009) for *E. marginatus*.

Avoiding predators is of paramount importance for fish larvae. In grouper early life stages, antipredator strategies are based on morphological features rather than swimming abilities (Russo *et al.*, 2009). It is therefore speculated that multifractality and anisotropy of swimming patterns observed in the present experiment are mainly explained in an optimal foraging theory framework. This study also confirms that the complexity of the swimming behaviour of fish larvae (*e.g.* MRW or even LW which is not the case in this study) may have direct ecological interpretation of small-scale processes. Consequently, observing foraging behaviour of fish larvae at small scales can provide new indicators of their strategy to explore their habitats. The MRW framework can be tested for other fish species with different prey types that can be encountered in the field. Additionally, future studies may also investigate any possible effect of fish larvae density on the complexity of their swimming behaviour as previously done on copepod behaviour (Dur *et al.*, 2011). This will require improvements to tracking systems for fish larvae, as they may be a limiting factor when the number of individuals is increased.

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