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Par

Mohamed-Sofiane MAHJOUB

Interactions prédateur-proie en milieu calme et milieu turbulent : études expérimentales sur des poissons planctonophages

Thèse dirigée par :
Sami SOUISSI / Jiang-Shiou HWANG / François. G. SCHMITT

Soutenance le 18 octobre 2010 à Keelung (Taiwan)
devant le jury composé de :

Chong Kim Wong, PR Chinese University of Hong Kong	Rapporteur
Myron Arms Peck, PR University of Hamburg	Rapporteur
Wen-Tseng Lo, PR National Sun Yat-Sen University	Examinateur
Sami Souissi, PR Université de Lille 1	Directeur de thèse
Jiang-Shiou Hwang, PR National Taiwan Ocean University	Directeur de thèse
François G. Schmitt, DR CNRS	Co-directeur de thèse
Syuhei Ban, PR University of Shiga Prefecture	Membre invité

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Résumé substantiel

Interactions prédateur-proie en milieu calme et milieu turbulent : études expérimentales sur des poissons planctonophages

Chez les poissons, l'amplitude du recrutement est déterminée par le succès alimentaire pendant la phase larvaire. Ainsi, la coïncidence spatio-temporelle du pic de production larvaire et du bloom planctonique est une condition *sine qua non* d'un bon recrutement. Récemment, de nombreuses études ont souligné le fait que les interactions entre niveaux trophiques du plancton se produisaient à l'échelle individuelle et non pas à l'échelle de la population. Dès lors, une compréhension des interactions prédateur-proie à l'échelle individuelle s'avère primordiale à la prédiction de la dynamique des populations marines exploitées.

Les relations prédateur-proie entre larves et juvéniles de poissons planctonophages d'une part, et de leurs proies planctoniques d'autre part, ont été étudiées expérimentalement. Dans un premier temps, nous avons réalisé des expériences de prédation à petite échelle pour étudier la flexibilité du comportement natatoire des larves de poissons ainsi que de l'effet du comportement des planctontes sur l'interaction prédateur-proie. Des techniques vidéo standard en 2D et 3D ont été utilisées pour déterminer les taux d'ingestion ainsi que les taux de capture à l'échelle individuelle. Les nages des prédateurs et de leurs proies ont été caractérisées par des descripteurs échelle-dépendants (vitesse, accélération, distance d'attaque, NGDR) et échelle-indépendants (dimension fractale et analyse multifractale). Les résultats ont montré que les larves du mérou malabar (*Epinephelus malabaricus*) passaient d'une nage anisotrope multifractale en absence de proies (*Artemia* sp.) à une nage isotrope orientée vers de petits volumes en présence de proies. Nos

résultats ont aussi montré que le comportement de nage affectait non seulement le taux de rencontre mais aussi le succès de capture. En effet, les trajectoires les plus complexes avec des distances d'attaque élevées ont été les moins fructueuses pour les larves du Corégone lavaret (*Coregonus lavaretus*). Enfin, l'étude de l'effet du comportement de nage des proies sur leur vulnérabilité à la prédation a confirmé les résultats théoriques selon lesquels les proies les plus rapides étaient les plus propices à la détection par les prédateurs. Ainsi, les femelles ovigères du copépode euryhalin, *Eurytemora affinis*, ont été les plus vulnérables à la prédation par leurs prédateurs naturels dans l'estuaire de la Seine, les larves de bar *Dicentrarchus labrax*. La deuxième partie de ce travail a été dédiée à l'étude expérimentale en grand volume de l'effet de la turbulence sur les performances de prédation des larves et juvéniles de bar exposés à des densités en proies réalistes. Cette étude a révélé que la turbulence était préjudiciable aux taux d'ingestion ainsi qu'au nombre maximal de proies ingérées quand les proies proposées étaient non-évasives (*Artemia*). Quand les prédateurs ont été confrontés à des proies évasives (copépodes vivants), les niveaux intermédiaires de turbulence se sont révélés bénéfiques.

摘要

本論文實驗觀察了仔稚魚與他們浮游性活餌間的『掠食-活餌』互動作用。首先，本研究利用小尺度的掠食實驗來觀察仔稚魚搜尋行為的靈活性與其影響的浮游生物之游泳行為在『掠食-活餌』中的互動。本論文使用了平面 (2D) 與立體 (3D) 錄影技術來觀察每一隻仔稚魚的攝食速率與捕食成功率。掠食者與活餌的游泳行為模式分成刻度-相依 (速度、加速、固定距離、淨/總移位比率) 與刻度不相依 (碎形尺度、多維碎形分析) 兩大項目進行量化處理。結果顯示仔稚魚會轉換其搜尋行為，從沒有活餌情況下的各向異性多維碎形模式變成有活餌情況的等向性模式。這個結果符合過去的報告所呈現，於自然環境下浮游性活餌的行為模式為多維碎形不勻稱分佈。本實驗亦發現游泳行為不僅決定了兩者間的遭遇率，也決定了捕食的成功率。事實上，不複雜的追擊行為配合短距離的攻擊模式大大的增加了捕食的成功率。調查結果發現，活餌的游泳行為在與掠食者之互動中是容易招致傷害的，本論文的實驗也證實了先前的理論研究，快速移動的活餌比慢速移動的活餌容易被看見而招致被捕食。在第二部份，大刻度的實驗其目的在於闡明亂流對於仔稚魚捕食成功表現的影響。從胃內容物分析結果發現，仔稚魚在捕食不會躲避的餌食 (*Artemia* sp. 與死的橈足類) 條件下，增加亂流對於浮游性掠食者的攝食率有負面的影響，本實驗結果顯示亂流也衝擊了最大食物攝取量。反過來說，仔

稚魚在捕食會躲避的活餌條件下，和緩的亂流對於仔稚魚的攝食率有正面的助益。

關鍵詞：浮游生物, 仔稚魚, 行為, 亂流, 瑪拉巴石斑, 歐洲真白鮭, 歐洲舌齒鱸, 豐年蝦 (*Artemia* sp.), 真寬水蚤 (*Eurytemora affinis*), 橈足類, 掠食行為.

Abstract

Predator-prey interactions under calm and turbulent conditions: experimental studies on planktivorous fish

We experimentally investigated the predator-prey interactions between larval and juvenile fish and their zooplanktonic prey. At first, we conducted small-scale predation experiments to investigate the flexibility of fish larvae search behavior as well as the effect of plankters' swimming behavior on the predator-prey interaction. 2D and 3D video techniques were used to investigate the ingestion rate and the capture success at the individual level. Swimming patterns of both predators and prey were quantified using both scale-dependent (speed, acceleration, fixation distance, net to gross displacement ratio) and scale-independent (fractal dimension, multifractal analysis) metrics. Results revealed that fish larvae switched from an anistropic multifractal search pattern in absence of prey to an isotropic spatially-restricted search behavior when prey were present. We also demonstrated that swimming behavior not only governed the encounter rate but also the capture success. In fact, less complex pursuits associated to attacks triggered from short distances yielded the highest capture successes. The investigation of the effect of *Eurytemora affinis* swimming behavior on the vulnerability to *Dicentrarchus labrax* larvae predation corroborated previous theoretical studies that faster prey are more conspicuous to predation than slower ones. In a second part of this work, we conducted larger scale experiments aiming at the elucidation of the effects of turbulence on the feeding success of fish larvae offered realistic prey densities. The results of gut contents analysis of larval sea bass feeding under increasing turbulence levels revealed that turbulence had negative effects on the feeding rates and maximum food intake of planktonic predators when preying on a non-evasive prey (*Artemia* sp.). Conversely, when feeding on an evasive prey (live copepod), moderate turbulence (*Re* $\approx$ 20000) was beneficial to juvenile sea bass.

Key words: zooplankton, fish larva, behavior, turbulence, malabar grouper, European whitefish, European sea bass, *Artemia* sp., *Eurytemora affinis*, copepod, predation.

Résumé

Les relations prédateur-proie entre larves et juvéniles de poissons d'une part et proies planctoniques d'autre part ont été étudiées expérimentalement. Dans un premier temps, nous avons réalisé des expériences de prédation à petite échelle pour étudier la flexibilité du comportement natatoire des larves de poissons ainsi que l'effet du comportement des zooplanctonctes sur l'interaction prédateur-proie. Des techniques vidéo standard en 2D et 3D ont été utilisées pour déterminer les taux d'ingestion ainsi que les taux de capture à l'échelle de l'individu. Les nages des prédateurs et des proies ont été caractérisées par des descripteurs échelle-dépendants (vitesse, accélération, distance d'attaque, NGDR) et échelle-indépendants (dimension fractale et analyse multifractale). Les résultats ont montré que les larves de mérou passaient d'une nage anisotropique multifractale en absence de proies, à une nage isotropique orientée vers de petits volumes en présence de proies. Ce comportement servirait à optimiser les taux de rencontre dans le milieu naturel où les proies sont distribuées de manière multifractale. Nos résultats ont montré que le comportement de nage des larves de Corégone affectait non seulement le taux de rencontre mais aussi le succès de capture. En effet, les trajectoires les plus complexes avec des attaques lointaines étaient les moins fructueuses. Enfin, l'étude de l'effet du comportement de nage du copépode *Eurytemora affinis* sur sa vulnérabilité à la prédation a confirmé les résultats théoriques selon lesquels les proies les plus rapides seraient les plus susceptibles à être détectées par les prédateurs. La deuxième partie de ce travail a été dédiée à l'étude expérimentale en grand volume de l'effet de la turbulence sur les performances de prédation des larves de poissons. L'étude des contenus stomacaux de poissons exposés à des niveaux de turbulence croissants ont révélé que la turbulence était préjudiciable aux taux d'ingestion quand les proies proposées étaient non-évasives (*Artemia* sp.). De plus, il a été démontré que la turbulence réduisait les maxima des taux d'ingestion par les larves de poissons. Enfin, quand les prédateurs sont présentés à des proies évasives (copépodes vivants), les niveaux intermédiaires (*Re* ≈ 20000) de turbulence ont été bénéfiques. En effet, à des niveaux turbulents intermédiaires, les avantages dus à la diminution de la capacité de perception chez les proies semblent dépasser les inconvénients de la diminution du succès de poursuite.

Mots clés : zooplancton, larve de poisson, comportement, turbulence, mérou malabar, Corégone lavaret, bar, *Artemia* sp., *Eurytemora affinis*, copépode, prédation.

Host laboratories

Laboratoire d'Océanologie et de Géoscience

CNRS UMR 8187 LOG

Université des Sciences et Technologies Lille 1

Station Marine de Wimereux

28 Avenue du Maréchal Foch, BP-80, 62930 Wimereux. FRANCE

&

Institute of Marine Biology

National Taiwan Ocean University

2 Pei-Ning Road, 202 Keelung. TAIWAN

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ν	kinematic viscosity
°C	Celcius, degrees
$\mu E\ s^{-1}\ cm^{-2}$	microEinstein per second per square centimeter
$\mu E\ s^{-1}\ m^{-2}$	microEinstein per second per square meter
μm	micrometer
2D	two dimensions
3D	three dimensions
$cm\ s^{-1}$	centimeter per second
cm	centimeter
CV	coefficient of variation
Hz	Hertz
km	kilometer
km^2	square kilometer
L	liter
L^{-1}	per liter

m s^{-1}	meter per second
m s^{-2}	meter per square second
mL	milliliter
mm	millimeter
mm s^{-1}	millimeter per second
mm s^{-2}	millimeter per square second
n	sample size
PVC	polyvinyl chloride
Re	Reynolds number
s	second
s.d.	standard deviation
s.e.	standard error
St	Stockes number
v	volt
W Kg^{-1}	watt per kilogram
W	watt

Chapter 1. General introduction and thesis outline

1.1 Larval fish, prey and encounters

Feeding success is essential for the development and survival of larval[1] fish (Legget and Deblois, 1994; Rao, 2003). A comprehensive understanding of the predator-prey interactions in the plankton is therefore a requisite to predict the recruitment of fish species. In 1990, Cushing updated the “match-mismatch” theory that explains the inter-annual variability of fish recruitment (Cushing, 1990). According to this author, a temporal match of maximum food availability with the spawning peak of a given species results in a good cohort survival, whereas a mismatch results in an unsuccessful recruitment (Cushing, 1990). Subsequently, numerous authors revealed that spatial match was also important for successful recruitment. For example, Lasker (1975) revealed the importance of water stratification and introduced the stable ocean hypothesis Lasker (1981). Later, Sinclair (1988) stated the member vagrant hypothesis that emphasized the importance of spatial retention of individuals in the regulation of a population size. Numerous *in situ* studies demonstrated the necessity of phytoplankton blooms for survival of fish larvae (e.g. Basilone *et al.*, 2004). However, most of these studies were based on sampling methods which integrate large volumes, irrelevant to plankters’ ambit (Pepin, 2004). Relying on such data to investigate the biological interactions between trophic levels, implicitly assumes a homogeneous distribution of both predators and their prey. Nevertheless, this approximation has been invalidated by fine scale studies (Paul and Paul, 1996; Young *et al.*,

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[1] Throughout this dissertation we will refer to pre-flexion and post-flexion fish as larvae. Sexually immature individuals having the meristic characteristics of adults will be referred to as juveniles (Kendall *et al.*, 1984).

2009). Observations at scales orders of magnitude higher than the environment actually perceived by plankters may result in a misleading understanding of the role and dynamics of the plankton in aquatic ecosystems (Kiørboe, 2008). The investigation of the predator-prey interaction should, therefore, be analyzed at the individual-scale (Pepin, 2004).

The main functions of a larval fish are to encounter food and to avoid being eaten. These two functions are interrelated. As an example, we may cite the report of Baumann *et al.* (2007) combining laboratory and field observations to reveal that poor feeding grounds led to starvation in early juveniles of sprat *Sprattus sprattus* (L.), rendering them more vulnerable to predation. Accordingly, fish larvae fitness is mainly dependent on encounter rates. At the individual scale, encounters depend on motion which can be i) inherent to the swimming behavior of the organism or ii) forced by ambient turbulence.

Many authors theoretically investigated the effects of both swimming behavior (Gerritsen and Strickler, 1977; Uttieri *et al.*, 2007a; Cianelli *et al.*, 2009) and turbulence (Lewis and Pedley, 2000; Galbraith *et al.*, 2004; Pécseli *et al.*, 2010) on the contact rates. While authors usually acknowledged that the encounter rates are not necessarily comparable to the ingestion rates (MacKenzie *et al.*, 1994; MacKenzie and Kiørboe, 2000), it has been implicitly assumed that the contact rates are equivalent to the encounter rates. However, numerous studies highlighted that predators' perceptive abilities are dependent on prey movement (Wright and O'Brien, 1982; Kiørboe and Visser, 1999). That is to say that two prey items located at the same distance from the predator have different probabilities of being perceived depending on their motion behavior. In order to get appropriate model inputs, it is therefore warranted to first empirically assess parameters with straightforward ecological significance like capture success and ingestion rates.

The ultimate objective of a predator is not only limited to prey encounter, but also to prey ingestion. Here again, combined effects of behavioral adaptations of both prey (Titelman and Kiørboe, 2003) and predators (Wanzenböck, 1992; Coughlin, 1993; Pasternak *et al.*, 2006), as well as turbulence-induced motion (MacKenzie *et al.*, 1994; MacKenzie and Kiørboe, 2000) govern the outcome of the post-encounter processes.

1.2 Thesis overview

The first purpose of this thesis is to provide a concise literature review of the role of plankters' motion (both behavioral and turbulence-driven) in the predator-prey interaction. This review only focuses on the results of empirical and theoretical studies performed at the individual level. The experimental part of this study was aimed at a global investigation of several aspects of the predatory sequence of larval fish. Namely, we investigated the effects of fish larvae swimming behavior and turbulence on the predatory sequence of larval fish when feeding on zooplanktonic prey. For each objective, we selected our target species according to their compatibility to the study. Selection criteria included the tolerance of the species to laboratory conditions as well as its ecological importance. We combined both small- and large-scale experimental approaches. First, we investigated the predator-prey interaction using video recordings at the individual small-scale (<5 L) in calm water. Second, we performed larger scale (250 L) predation experiments aimed at the study of the effects of turbulence on larval and juvenile fish feeding efficiency.

Theoretical studies predicted that different swimming strategies lead to different encounter rates, with some strategies being more advantageous under specific prey distribution patterns (Uttieri *et al.*, 2007b; Cianelli *et al.*, 2009). In order to maximize encounters in a changing prey environment, a fish larva should accordingly rely on a flexible search behavior. Our first experimental objective was, therefore, to test for the flexibility of larval fish swimming behavior in response to prey availability. Zooplankters' behavior does not only affect encounter rates, but also the whole predator-prey interaction outcome. We consequently investigated the outcome of the predator-prey interaction in response to the swimming behavior of both predators (fish larvae) and prey (zooplankton), respectively. Finally, because the predator-prey interactions are also affected by turbulence, we experimentally investigated the role of turbulence on fish larvae and juveniles feeding rates on both non-evasive (*Artemia* sp. and dead copepods) and evasive prey (live copepods).

Specifically, the following studies have been undertaken to fulfill the above stated objectives:

1) Role of swimming behavior and turbulence in the predator-prey interaction: A literature review;
2) Swimming behavior of Malabar grouper (*Epinephelus malabaricus*) larvae in response to *Artemia* sp. availability;
3) Swimming behavior and capture success in European whitefish (*Coregonus lavaretus*) larvae on zooplanktonic prey;
4) Swimming kinematics of *Eurytemora affinis* (Copepoda, Calanoida) reproductive stages and differential vulnerability to predation of larval *Dicentrarchus labrax* (Teleostei, Perciformes);
5) Negative effects of turbulence on the feeding dynamics in European sea bass (*Dicentrarchus labrax*) larvae on *Artemia* sp. nauplii;

6) The effects of turbulence on the feeding in sea bass juveniles on live versus dead *Eurytemora affinis* (Copepoda, Calanoida).

Chapter 2. Role of swimming behavior and turbulence in the predator-prey interaction: A literature review

2.1 Introduction

Fish larvae responses to biotic and abiotic factors are not only species- but also stage-specific. For instance, morphological modifications during ontogeny are associated with important changes in swimming performance (Clark *et al*., 2005; Peck *et al*., 2006; Georgalas *et al*., 2007), foraging behavior (Houde and Schekter, 1980; Hunt von Herbing and Gallager, 2000; Anneville *et al*., 2007b), optimal prey to predator size ratio (Munk, 1992), trophic niche breadth (Dickmann *et al*., 2007; Young *et al*., 2010) and starvation resistance (Molony, 1996). In addition, maternal condition may also affect larval fish performance (Browman *et al.*, 2003). Finally, even fish belonging to the same cohort and egg batch can exhibit extremely variable behaviors (Browman *et al.*, 2003). All these factors may act in synergy and influence larval foraging behavior rendering the investigation of the planktivory behavior very complex. Reviewing all the above cited effects is beyond the scope of our work. Herein, we aim at providing the reader with some essential background information to understand the effects of individual plankters' motion on the foraging success of larval fish.

2.2 Role of swimming behavior in the predator-prey interaction

The swimming performance in fish is a function of both intrinsic and extrinsic factors. As a larva grows, and its swimming velocity increases, its Reynolds number (*Re*, ratio of inertial forces to viscous forces) increases. Thus, the fish will be successively confronted to viscous, transitory and inertial realms. However, *Re* not only depends on fish size and speed but also on ambient fluid viscosity, which is determined by salinity and, to a higher extent, by temperature (Hunt von Herbing, 2002). In fact, higher temperatures decrease the kinematic viscosity of the water which increases *Re*. As a matter of fact, fish larvae and juveniles display higher swimming speeds when temperature increases (Hunt von Herbing and Keating, 2003; Peck *et al*., 2006). Similarly, warm-water species are more efficient swimmers than cold-water species (Leis, 2007). Indeed, warm-water species are able of much larger displacements than cold-water species (Leis, 2007), which is attributed not only to the relative easiness of swimming in less viscous water but also to the higher efficiency of muscles in warmer water conditions (Hunt von Herbing, 2002).

In the planktonic realm, a predator's fitness depends mainly, but not exclusively, on its encounters with prey, mates and predators (Kiørboe, 2008). Planktonic predators have been reported to perceive their prey through vision (Strickler *et al.*, 2005), mechanoreception (Govoni *et al.*, 1986; Hwang *et al.*, 1994) and chemoreception (Tiselius and Jonsson, 1997; Tanaka *et al.*, 1991; Knutsen, 1992). Nevertheless, fish larvae are basically visual predators (Hunter, 1981). A large body of literature was devoted to the portrayal of the feeding behavior of fish larvae, and the three following foraging strategies have been described:

- Ambush strategy: predators that attack prey at the edge of their detection range. This type of predators only moves occasionally.

- Cruise strategy: predators like herring (MacKenzie and Kiørboe, 1995) and clown fish (Coughlin *et al.*, 1992) that search and attack the prey while swimming (Galbraith *et al.*, 2004).

- Pause-travel (salutatory) strategy: predators like cod (MacKenzie and Kiørboe, 1995) and sea bass (Georgalas *et al.*, 2007) that search for prey while stationary (not actively swimming). These predators usually attack their prey during the pause (Galbraith *et al.*, 2004). It is worth pointing out that some authors suggested that the notion of the pause-travel search as a distinct foraging strategy needs to be re-considered. Indeed, they argued that there is a continual change from the ambush strategy to the cruise search strategy with increasing duration of swimming events between pauses (Dowling *et al.*, 2000).

Once the larval search strategies revealed, experimental efforts were oriented toward the depiction of the larval fish predation sequence. Most authors agreed on the following successive events during a successful predation sequence: encounter, pursuit, fixation, attack, capture and ingestion (MacKenzie *et al.*, 1994; Rao, 2003). Gerritsen and Strickler (1977) were the first to model the predator-prey interaction. This pioneer model was based on a number of approximations. In fact, it was based on the assumptions of a spherical perceptive field, a homogeneous prey distribution and a constant search pattern irrespective of prey availability. However, field and laboratory data showed that these hypotheses are not valid. First, empirical evidence emerged that the perceptive area in fish larvae is not spherical (*e.g.* Coughlin, 1993). Second, a patchy distribution pattern of prey has been consistently reported from fine scale studies (Paul and Paul, 1996; Young *et al.*, 2009). Finally, video observations of larval fish swimming patterns revealed that foraging behavior is flexible to prey density (Munk and Kiørboe, 1985; Coughlin *et al.*, 1992). Subsequent theoretical effort was therefore oriented toward the improvement this predator-prey model by taking into account different reactive shapes for the predator (Galbraight *et al.* 2004), patchy distribution patterns of prey (Uttieri *et al.*, 2007a), and different search strategies (Cianelli *et al.*, 2009). All of these investigations confirmed that different behaviors accounted for different outcomes of the predator-prey interaction.

In what follows, we will review the role of larval fish swimming behavior during the predatory sequence on the feeding success. During all these events, the planktonic prey may detect the predator and elicit an escape response. The efficiency of this response depends on its timing (Titelman, 2001), speed (Titelman, 2001) and direction (Caparroy *et al.*, 2000).

2.2.1 Role of swimming behavior in encounter

Intuitively, different search strategies may lead to different contact rates. Theoretical approaches help resolving such issues. From the mechanistic perspective, an increased activity results in higher contact rates (Gerritsen and Strickler, 1977). Conversely, faster predators produce higher mechanical disturbance and are detected at a higher distance than slow moving ones (Kiørboe and Visser, 1999; Visser, 2001). Lewis and Pedley (2000) predicted that changes in predator direction during search could be detrimental because they lead to an overlap in the scanned volume. However, this hypothesis can only apply in a static prey field, which is unlikely to occur in nature. Indeed, numerous empirical observations (Coughlin *et al.*, 1992; Uttieri *et al.*, 2007b) and theoretical simulations (Cianelli *et al.*, 2009) demonstrated that more convoluted swimming paths enhance contact rates for predators, especially when food concentrations are high (Uttieri *et al.*, 2007a) and distributed in patches (Cianelli *et al.*, 2009). Within prey patches, Garcia *et al.* (2007) demonstrated that displaying turning angles taken from exponential distributions optimizes encounters.

2.2.2 Role of swimming behavior in pursuit success

Experimental results revealed that faster pursuits are more likely to result in higher capture success because of the reduction of the time available to the prey to detect and escape from the predator (Wanzenböck, 1992). However, while intensive research effort was devoted to the role of path complexity on the encounter rates, there is surprisingly no available data on the effect of the pursuit complexity on the outcome of the pursuit.

The fixation is the interruption of the pursuit and the aiming at the prey that usually precedes an attack (Wanzenböck, 1992). In larval cyprinids, the duration of the fixation time is inversely proportional to capture success (Wanzenböck, 1992). Indeed, the longer the predator will stay in vicinity of the prey, the higher the chances of being detected will be. The fixation distance, is also important for the larval feeding success. In fact, the shorter the fixation distances, the higher the chances of successful attack (Viitasalo *et al.*, 1998; MacKenzie and Kiørboe, 2000). In fact, according to Viitasalo *et al.* (1998) and MacKenzie and Kiørboe (2000) the ability of the larval fish to approach the prey without triggering an escape response is the main mechanism leading to a successful attack.

2.2.3 Role of swimming behavior in attack and capture success

Factors like the strike speed (Drost and Van Den Boogaart, 1986; Drost, 1987) and the aptitude of the larvae to create a suction flow (Drost and Van Den Boogaart, 1986; Coughlin, 1994) were reported to enhance the efficiency of the attack. The angle of the attack is also important; in fact larval stages of many planktivorous fish species preferably attack their prey from below in order to avoid being perceived (Coughlin, 1993; Thetmeyer and Kils, 1995). This shows the existence of differential feeding strategies on the vertical and horizontal projections. Interestingly, very few studies investigated the anisotropy (*i.e.* differences in the swimming properties on different projections) of larval fish swimming behavior.

2.3 Role of turbulence in the predator-prey interaction

Water flow is a common physical trait of aquatic environments. Depending on the properties of the water current, we distinguish laminar and turbulent flows. A laminar flow is characterized by parallel streamlines and an almost constant fluid velocity, whereas a turbulent flow exhibits random fluctuations of velocity magnitude and direction. A turbulent flow is composed of whirls (eddies) of different sizes. The largest whirls have a length scale *L* comparable to the cross section of the water flow. The big whirls are unstable and break up into smaller whirls to which they transfer their energy. These small whirls also beak up into smaller whirls and so on. When the fluid viscosity is sufficient to dissipate the cascading energy, the whirls become stable. This smallest scale of whirls is called the Kolmogorov scale (Pope, 2000). In open ocean, the Kolmogorov scale ranges from 0.1 mm to 10 mm (Hill *et al.*, 1992).

At large scales, water masses movement may affect larval fish distribution (Descroix *et al*., 2005; Lo *et al*., 2010). At the scale of a planktonic organism, two cases are observed. In fact, laminar flow does not generate any difference in the contact rates because the plankter is trapped into the flow (Kiørboe, 2008). Conversely, in a turbulent flow characterized by the existence of velocity gradients, contact rates are enhanced (Schmitt and Seuront, 2008). It is therefore important to characterize the flow in order to accurately assess its effects on the predator-prey interaction. The flow nature is determined by its Reynolds number (*Re*).

$$\mathrm{Re} = \frac{U \times L}{\nu} \quad (1)$$

where *U* and *L* are the typical velocity and dimension scales (dimensions of the system) and ν the kinematic viscosity, respectively. The critical *Re* value above which a flow is considered turbulent depends on the geometry of the system. In open channels (*e.g.* rivers), turbulent flows have *Re* values > 1000.

Flow is also characterized by its turbulent velocity *u'* which is estimated following Tennekes and Lumley (1972) under the assumption of isotropic fluctuations:

$$u' = \sqrt{< V^2 > - V_0^2} \qquad (2)$$

where V and V_0 are the velocity component in the direction of the flow and the mean velocity, respectively. The triangular brackets, < >, mean "average of".

The amount of energy lost due to viscous forces is the dissipation rate (ε) in W kg^{-1} (or m^2 s^{-3}). It can be estimated as following Kolmogorov (1941 *in* Kolmogorov, 1991):

$$\varepsilon = \frac{u'^3}{L} \qquad (3)$$

In the aquatic environments, turbulence is ubiquitous, it therefore affects plankton behavior (Costello *et al.*, 1990; Hwang, 1991; Hwang and Strickler, 1994), feeding (Saiz *et al.*, 2003), growth (Saiz and Alcaraz, 1991) and also distribution (Franks, 2001; Metaxas, 2001). The role of turbulence on predator-prey interactions has been largely evaluated from both theoretical approaches (MacKenzie *et al.*, 1994; Seuront *et al.* 1999; Lewis and Pedly, 2001; Fiksen and MacKenzie, 2000; Megrey and Hinckley, 2001; Galbraith *et al.*, 2004; Lewis and Bala, 2006; Pécseli *et al.*, 2010) and laboratory experimentations (MacKenzie and Kiørboe, 1995; MacKenzie and Kiørboe, 2000; Utne-Palm and Stiansen, 2002; Utne-Palm, 2004; Kato *et al.*, 2008). These studies revealed that turbulence mostly affects the meso-sized (mm to cm) predators, whereas it has less impact on smaller and larger predators (Kiørboe and Saiz, 1995). We hereafter review the effects of the turbulence on the predatory sequence.

2.3.1 Role of turbulence in encounter

2.3.1.1 Direct effects

Since the paper of Rothschild and Osborn (1988), turbulence has been acknowledged to enhance encounter rates by transporting more prey items into the perceptive field of the predators. This result got support from subsequent theoretical investigations (MacKenzie *et al.*, 1994; Kiørboe and MacKenzie, 1995; Lewis and Pedley, 2000; Pécseli *et al.*, 2010). Later, Schmitt and Seuront (2008) showed that contact rates in the plankton may be much higher than what was previously reported. The rationale is that turbulence creates patchiness in particle distributions: the preferential concentration effect (Maxey, 1987). In fact, particles in a fluid behave according to their inertia which is measured in terms of Stokes number (St). For St>>1, particles are unaffected by turbulent eddies and for St<<1 particles behave as flow tracers. For transitional St, particles do not follow high vortices but can respond to some fluid motions. Dense particles could be ejected from high vorticity regions and are concentrated in high strain rate regions. This phenomenon, also known as preferential concentration, has been verified for heavy particles (Maxey, 1987; Squires and Eaton, 1991; Wang *et al.*, 2000) and for neutrally buoyant particles that have a size and density comparable with those of copepods (Schmitt and Seuront, 2008).

The relative turbulence-induced increase in contact rates is dependent on the size and the behavior of predators. First, turbulence effects are only relevant to meso-sized (mm-cm) predators (Kiørboe and Saiz, 1995). In fact, while prey smaller than the Kolmogorov scale are caught inside eddies and are relatively unaffected by velocity gradients, larger predators have swimming speeds which allow them to overcome turbulent velocities (Kiørboe, 2008). Second, maximum benefits are observed for pause-travel searchers (MacKenzie and Kiørboe, 1995) and for predators with long reaction distances (Kiørboe and Saiz, 1995). Finally, for a predator to achieve an optimal foraging behavior, modelling efforts revealed that swimming speed should decrease with increasing turbulence so that foraging remains energetically favorable (Pitchford *et al.*, 2003).

Turbulence is not always beneficial. In fact, the actual benefits of turbulence are decreased when models are parameterized with realistic search volume shapes (Lewis, 2003; Galbraith *et al.*, 2004). Finally, turbulence may distort signals emitted by prey and thus reduce the detection capacities of the predator (Saiz *et al.*, 1992; Yen *et al.*, 2008).

2.3.1.2 Indirect effects

Franks (2001) suggested that turbulence may indirectly affect contact rates in the plankton. Indeed, *in situ* reports indicate that copepods can avoid the mixed layers and sink deeper in the water column during turbulence events (Haury et al., 1990; Mackas *et al.*, 1993; Incze *et al.*, 2001). Similarly, fish larvae of several species have been reported to migrate towards the bottom during strong wind events (Lough and Mountain, 1996; Hillgruber and Kloppmann, 2000; Reiss *et al.*, 2002). According to Franks (2001), the turbulence avoidance behavior, leads to enhanced concentrations of both larval fish and their prey below the mixed layer resulting in higher encounter rates.

2.3.2 Role of turbulence in pursuit success

Detrimental effects of turbulence on the pursuit success have been revealed by analytical exercises (Mackenzie and al., 1994; Kiørboe and Mackenzie, 1995; Kiørboe and Saiz, 1995; Fiksen and MacKenzie, 2000; Mariani *et al.*, 2007) and empirical studies (Mackenzie and Kiørboe, 2000). The rationale is that at high levels of turbulence, prey are swept away from the perceptive area of the fish faster than the reaction of the fish, leading to unsuccessful pursuits (Mackenzie and Kiørboe, 2000).

2.3.3 Role of turbulence in attack and capture success

Turbulence leads to higher attack rates due to an enhancement of encounter rates (MacKenzie and Kiørboe, 1995; Utne-Palm and Stiansen, 2002). However, at high food abundances, experimental evidence exists that attack rates in turbulent and still water are comparable (MacKenzie and Kiørboe, 1995). As during pursuit, models predict that turbulence displaces prey items away from the predator before an attack is triggered (*e.g.* MacKenzie *et al.*, 1994; Lewis and Pedley, 2001).

Turbulence amplifies the relative velocity of a predator to its prey during the attack which may reduce the capture success (MacKenzie *et al.*, 1994; Kiørboe and Saiz, 1995) especially for species with high reactive distance (Lewis and Pedley, 2001). However, experimental studies on cod larvae revealed that attack success was very high for both low and high turbulence levels (MacKenzie and Kiørboe, 2000). These authors argued that the attack duration is negligible compared to the turbulent velocity and that turbulence-induced prey advection is of no consequence on attack success (MacKenzie and Kiørboe, 2000).

Chapter 3. Swimming behavior of Malabar grouper (*Epinephelus malabaricus*) larvae in response to *Artemia* sp. availability[2]

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[2] From: MAHJOUB M.-S., S. SOUISSI., G. DUR, F.G. SCHMITT, F.-H. NAN and J.-S. HWANG, (under revision) Effects of prey availability on the malabar grouper (*Epinephelus malabaricus*) larvae swimming behavior. *Hydrobiologia*.

3.1 Introduction

While feeding success is a requisite for larval recruitment (Heath, 1992; Legget and Deblois, 1994), field reported average prey concentrations are usually lower than those necessary to ensure larval survival (Jenkins, 1988). Recent individual-based models suggested that larval fish can survive, but suffer retarded growth at average prey concentrations reported from the field (Kuhn *et al.*, 2008). At the micro-scale level, prey densities have been reported to be highly variable (Owen, 1989) but often sufficient to support growth of many larval fish species (Paul and Paul, 1996). This discrepancy is due to the fact that most sampling methods (*e.g.* plankton nets) integrate large water volumes and hence exclude small scale processes, like patchiness, which are crucial for the predator-prey interaction (Pepin, 2004). Finding and foraging on food patches have been reported to be important for planktonic predators (Lasker, 1975; Lasker and Zweifel, 1978; Eldridge *et al.*, 1982; Mohammadian *et al.*, 1997), namely when prey densities outside patches are below the growth-threshold (Peck and Daewel, 2007). Because motion plays a central role in plankton encounter rates (Kiørboe, 2008), a flexible search behavior is fundamental for larval fish to take advantage of a changing prey availability (Munk, 1995). Indeed, fish larvae have been reported to change their swimming behavior according to the available prey density (Munk and Kiørboe, 1985; Coughlin *et al.*, 1992; Munk, 1995). Coughlin *et al.* (1992) suggested these changes to be behavioral responses intended to better exploit food patches.

As early as 1982, Strickler (1982) showed that gravity had important implications on the feeding currents of copepods and on their negative buoyancy. More recently, Schmitt and Seuront (2001), De Robertis *et al.* (2003), Nihongi *et al.* (2004) and Seuront *et al.* (2004b) noticed the existence of differences in the horizontal and the vertical projections (*i.e.* anisotropy) of the behavior of

Temora longicornis (Copepod), *Euphausia pacifica* (Euphausiid), *Daphnia pulex* (Cladocera) and *Leptodiaptomus ashlandi* (Copepod), respectively. For planktivorous fish, both adult (Janssen, 1981; Thetmeyer and Kils, 1995) and larval stages (Coughlin, 1993; Mahjoub *et al.*, 2008) have been reported to preferably detect and attack their prey from below, showing different feeding patterns in the vertical and horizontal planes. Schmitt and Seuront (2001) suggested considering behaviors on both vertical and horizontal planes as a starting point for the investigation of foraging strategies in the zooplankton. Interestingly, even a large body of literature revealed the existence of changes in the swimming behavior of fish larvae in response to prey availability (Munk and Kiørboe, 1985; Munk, 1995), very few works focused on comparing the vertical and horizontal views with respect to the search strategy in fish larvae. Here, we investigated the swimming patterns of malabar grouper, *Epinephelus malabaricus* Bloch and Schneider (1801), larvae in all of the vertical, horizontal and 3D projections in both absence and presence of prey. Our experiment aimed at investigating how malabar grouper changed its search strategy according to prey availability and whether the corresponding search behavior properties were identical on all projections (*i.e.* isotropic).

3.2 Material and methods

3.2.1 Experimental animals

21 days old larvae of Malabar grouper (*Epinephelus malabaricus*) were obtained from the Aquaculture Department of the National Taiwan Ocean University on May 2007. Larvae were kept in an aquarium filled with 25 L of filtered sea water (temperature: 26˚C; salinity: 35) and supplied with gentle air bubbling. Photoperiod was 12:12 (light:dark). Fish were fed daily with freshly hatched *Artemia* sp. Nauplii and the bottom of the tank was siphoned at the end of each day.

3.2.2 Experimental vessel size

The experimental vessel had to be small enough to ensure accurate definition of the video recordings but large enough to allow larval fish feeding. In order to fulfill the above stated compromise a 1 L (10 × 10 × 10 cm) experimental container was chosen. This size is unlikely to be sufficiently large to reflect the actual larval behavior observed in open ocean. However, it ensured the collection of trajectories long enough to have good estimates of fractal dimensions (see Table 3 in the results section). In addition, it remains reasonable to compare the swimming paths of larval fish recorded in the same vessel regardless of its size.

3.2.3 Video set-up

The experiments were carried out in a cubic glass vessel with black paper covering the bottom, and two adjacent lateral walls in order to enhance contrast with larvae. A 9W lamp (120 v, 60 Hz) suspended at 45 cm above the experimental tank provided the only light source. Two orthogonally placed HDD cameras (Sony SR100, 30 Hz) facing the two transparent sides were used to record the larval behavior in 2 orthogonal planes. For each experiment, flash lights were emitted before the acclimatization and after the recording period in order to mark the beginning and the end of both videos for synchronization purpose.

3.2.4 Experimental procedure

For each of the 3 replicates, a group of 4 fish larvae (25 days old, TL ± s.d. = 7.16 ± 1.0mm) randomly caught from the maintenance tank and starved for 2 hours was put in the experimental tank. Each test started with allowing the larvae to acclimatize for 15 min before their behavior was recorded for 20 min. Then, 100 freshly hatched *Artemia* sp. nauplii were gently added and the behavior was recorded again for 20 min after a second acclimatizing period of 10 min. The temperature, checked at the end of each experiment, was 27 ± 1.3˚C (mean ± s.d.).

3.2.5 Video analyses

The orthogonal cameras recorded the XY and the ZY perspectives with X and Z the two horizontal axes and Y the vertical one. For each replicate, videos from the two cameras were exported to the Adobe Premiere Pro 2.0 software (Adobe Premiere Pro, 2.0, Stingray) for synchronization by matching the starting and the ending frames previously marked by a flash of white light. Since no synchronizer was used, a time lag occurred between both videos and a manual synchronization was needed. Consequently, the playback duration of the longest sequence was adjusted so that the duration of both video sequences matched perfectly.

Synchronized videos were then overlapped in order to create a single third movie on which each animal could be seen from both lateral views. A thorough visioning of this video was performed to select valid paths for further analysis. We defined a suitable path as a trajectory occurring at least two body lengths away from any of the tank walls and being longer than 10 s (300 frames).

Selected sequences were subsequently saved as a succession of images for tracking which was achieved using the TrackIt V.2.0 (Net Tech Consulting, Iguana Gurus) software. This software allowed us to manually point the position of the larvae on each of the successive images constituting the selected sequences. As an output, each sequence resulted in a matrix containing the three spatial coordinates (x, y, z) of the larva over time.

3.2.6 Data analyses

3.2.6.1 Velocity (V)

Instantaneous 2D (V_{i2D}) and 3D (V_{i3D}) velocities were calculated between each two successive frames as follows:

$$V_{i2D} = \frac{\sqrt{(x_b - x_a)^2 + (y_b - y_a)^2}}{\Delta t} \tag{4}$$

$$V_{i3D} = \frac{\sqrt{(x_b - x_a)^2 + (y_b - y_a)^2 + (z_b - z_a)^2}}{\Delta t} \tag{5}$$

where x, y and z are the coordinates of the larva, a and b are two successive frames, and Δt the time step (0.03). For comparison between prey conditions, the mean velocity for each trajectory was first computed and then the means of all trajectories for each condition were computed. Velocities were estimated for both vertical and horizontal projections and for the overall 3D path.

3.2.6.2 Reynolds number (Re)

We estimated *Re* using the formula 1 (see chapter 2).

3.2.6.3 Net to Gross Displacement Ratio (NGDR)

If we consider the net displacement (N_d) as the distance between the starting and the ending point of a track, and the gross displacement (G_d) as the sum of the length of all the steps constituting the path, the NGDR is the ratio of N_d to G_d. NGDR values range from 0 to 1 with increasing path linearity. Because of the problems inherent to the scale-dependency of the NGDR (Seuront *et al.*, 2004b), we used a graphical method to compare the linear fits of the NGDR values across the first decade of time scales for both vertical and horizontal views.

3.2.6.4 Fractal dimension (D_f)

Fractal dimension D_f, is a dimensionless scale-independent metric that has been often used to describe zooplankton swimming trajectories (Coughlin *et al.*, 1992; Seuront *et al.*, 2004a; Uttieri *et al.*, 2007a). The accuracy of this method has been criticized (Normant and Tricot, 1991; Turchin, 1996; Halley *et al.*, 2004). We remind here that the main objective, as emphasized by Despland (2003), was to compare trajectories rather than to determine the exact fractal dimension of a given path. D_f was estimated using the classical box-counting method (*e.g.* Seuront *et al.*, 2004b; Mahjoub *et al.*, 2008). If we consider a 2D path plotted on a grid of squares of size λ, the number of squares occupied by the path when λ varies can be written:

$$N(\lambda) = k\lambda^{-D_f} \tag{6}$$

where k is a constant and the exponent D_f is the fractal dimension which is estimated by the slope of the power fit of the log-log plot of $N(\lambda)$ versus λ . In this framework, we used D_f to compare the complexity of the swimming paths projections in both vertical and horizontal views. In the case of such 2D projections, D_f ranges from the value of 1 for a linear path to 2 for a trajectory filling the entire plane.

3.2.6.5 Moment function of the displacements

The movements of planktonic organisms are usually reported to be intermittent (Schmitt and Seuront, 2001; Titelman and Kiørboe, 2003; Schmitt *et al.*, 2006; Alcaraz *et al.*, 2007). Such behavior leads to high inter- and intra-individual variance levels. In order to thoroughly examine the significance of such data, one should use, in addition to standard metrics, tools developed for the studies of intermittent phenomena. Here, we follow Schmitt and Seuront (2001; 2002) who first suggested a tool derived from turbulence studies to investigate plankton behavior at the individual scale: the moment function of the displacements.

If we consider ΔX_τ the displacement of a plankter during the time increment τ

$$\Delta X_\tau = X(t+\tau) - X(t) \tag{7}$$

The norm of this displacement in 3D is:

$$\|\Delta X_\tau\| = [(X(t+\tau)-X(t))^2 + (Y(t+\tau)-Y(t))^2 + (Z(t+\tau)-Z(t))^2]^{1/2} \tag{8}$$

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

$$< \|\Delta X_\tau\|^q > \approx \tau^{\zeta(q)} \tag{9}$$

Where $\zeta(q)$ is the scale-invariant moment function that characterizes the complexity of the lagrangian paths (Schmitt and Seuront, 2001). The slope of the power fit of the log-log plot of $< \|\Delta X_\tau\|^q >$ vs. τ for each q value provides $\zeta(q)$. The Scaling of the norm $< \|\Delta X_\tau\|^q >$ vs. τ for q = 1, 2 and 3 as well as the scaling of moment exponents $\zeta(q)$ for both treatments were computed using a custom program implemented in MatLab (7.5, The Math Works, inc.) by Dur *et al.* (2010).

When $\zeta(q) = q/2$ the path has the property of a normal (Brownian) diffusion for which displacements are normal random variables. Thus, they are characterized by their mean and variance. In this case there are many small displacements and very few large ones. When $\zeta(q) \neq q/2$ the walk belongs to anomalous diffusion, for which long displacements are more frequent than in Brownian case. If $\zeta(q)$ is non linear, then the walk is said to be multifractal and long displacements are more frequent than for the two previous cases (Bacry *et al.*, 2001; Schmitt and Seuront, 2001).

3.3 Results

3.3.1 Predator behavior

A total of 22388 data points were obtained, with 12740 data when prey was absent and 9648 data when prey was present.

3.3.1.1 Swimming paths

The observation of the video recordings revealed that grouper larvae adapted a pause-travel search strategy alternating short swimming bursts with motionless pauses. Space utilization was different depending on prey availability. When there were no prey, the larvae swam more actively on the vertical plane and limited their horizontal displacements ensuring higher space occupation on the vertical axis. When prey were present, the larvae focused on smaller water volumes and did not seem to have any preference for either the vertical or the horizontal plane within that search area (Fig. 1).

3.3.1.2 Mean Swimming Velocity

Prey availability had an effect on the computed mean swimming speeds. In fact, larvae were faster when prey were absent (Fig. 2). However, speed difference was only statistically significant for the XY vertical projection (Table 1, Wilcoxon, $p < 0.05$).

Velocities estimated from 2D projections underestimated the actual 3D speeds (Fig. 2). This underestimation was higher in the horizontal projection when compared to those observed in the vertical views. This confirms that swimming paths are anisotropic, with movements being more complex on the vertical axis.

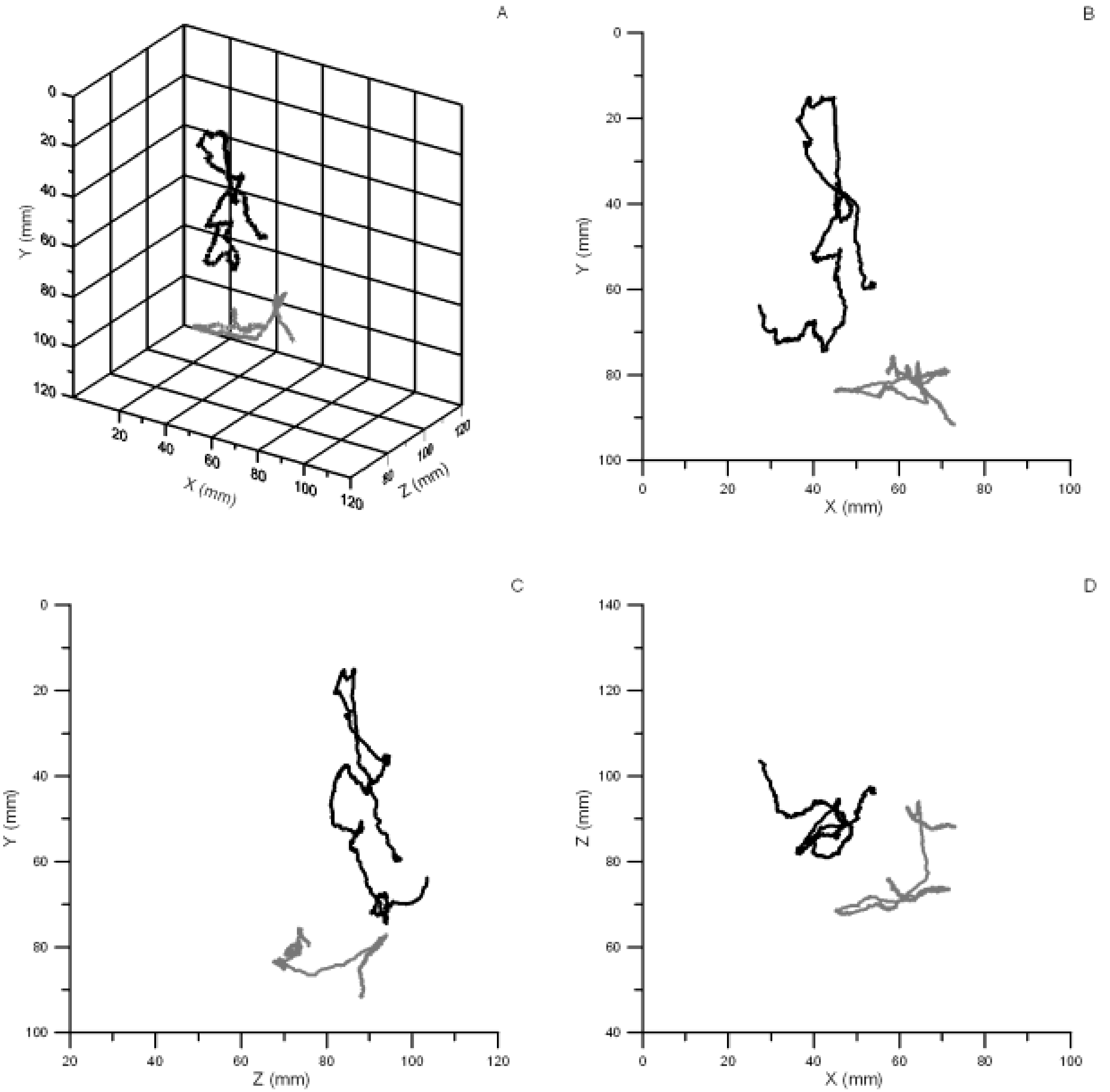

Fig. 1. **Two typical swimming paths of grouper larva (*Epinephelus malabaricus*) in absence (black) and in presence of *Artemia* (grey) in 3D (A), on the vertical plane XY (B), on the vertical plane ZY (C) and on the horizontal plane XZ (D). Both paths are 42 s in duration (n = 2).**

3.3.1.3 Reynolds number

The *Re* of the larvae decreased from 55.1 when prey was absent to 45.4 as prey were added. In other words, the larvae were confronted to a less viscous realm when prey were absent.

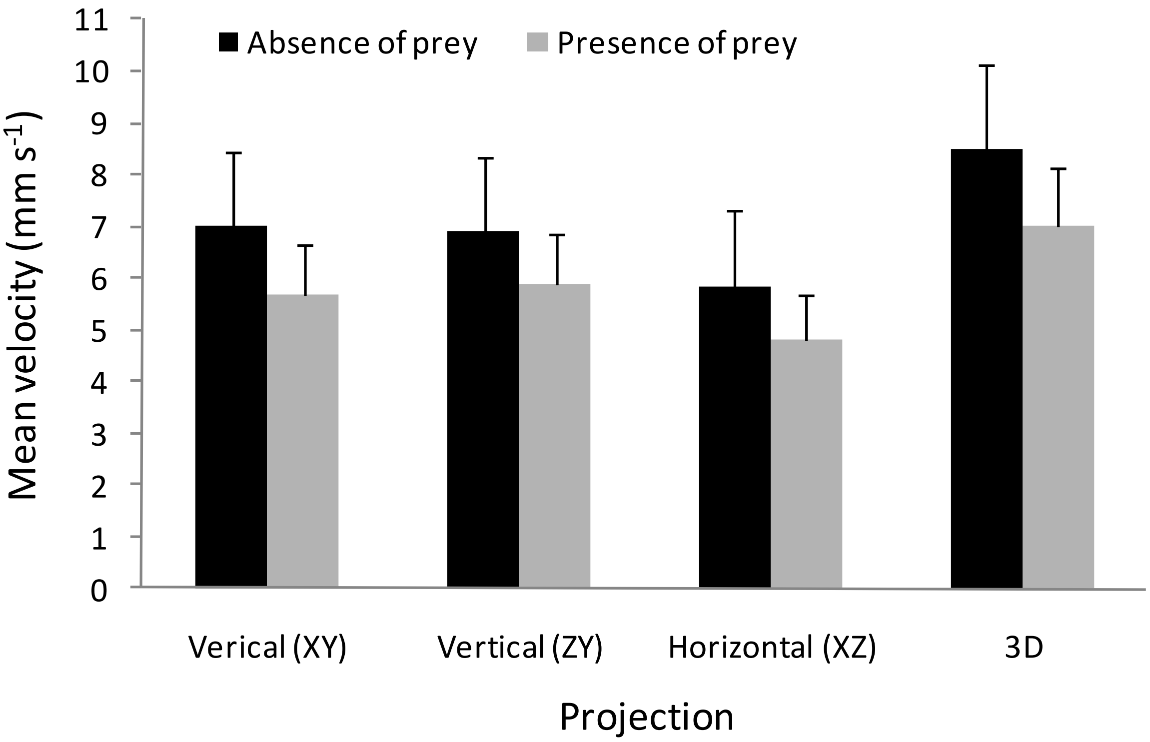

Fig. 2. Mean (± s.d.) velocities of the vertical projection, horizontal projection and in 3D of larval grouper for both prey conditions. The star indicates significant difference at $p < 0.05$.

3.3.1.4 Swimming complexity

Net to Gross Displacement Ratio (NGDR)

The scaling of the NGDR for the different projections and for both prey conditions are shown in Fig. 3. The corresponding statistics of the fit on a log-log plot over the first decade of time scales (0.04 s to 0.4 s) are shown in Table 2. Fig. 3 shows that the NGDR values were higher when prey was present, implying higher turning rates in the absence of prey. No differential behavior between the projections could be inferred from NGDR analysis.

Table. 1. **Comparative statistics between the two prey conditions for the averaged mean speeds of each trajectory. Horizontal (XY): horizontal projection without prey vs. horizontal projection with prey; Horizontal (ZY): horizontal projection without prey vs. horizontal projection with prey; Vertical: vertical projection without prey vs. vertical projection with prey; 3D: 3D without prey vs. 3D with prey. Sample size (n = 20) consists of the total number of trajectories.**

View	p value	n
Vertical (XY)	0.033	20
Vertical (ZY)	0.086	20
Horizontal (XZ)	0.057	20
3D	0.057	20

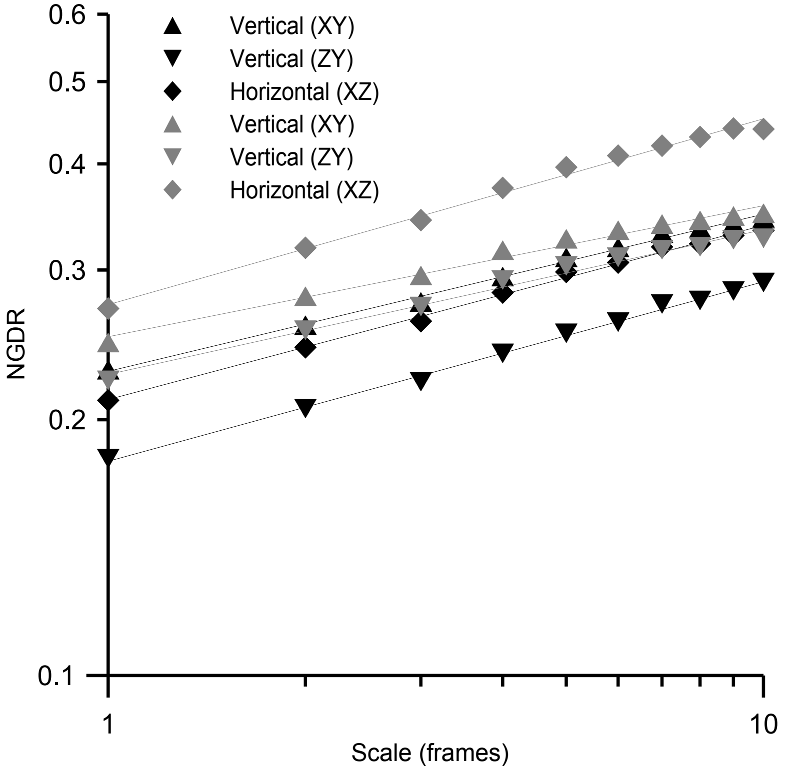

Fig. 3. **Average NGDR of all trajectories, at different scales, in both absence (black) and presence of prey (grey). Solid lines represent the power fits for each scaling data.**

Table. 2. **Statistics of the power fit to the NGDR scaling for both prey conditions.**

Prey condition	Projection plan	R^2	p value
Without prey	Vertical XY	0.99	0.95×10^{-4}
	Vertical ZY	0.99	0.79×10^{-4}
	Horizontal XZ	0.99	0.11×10^{-4}
With prey	Vertical XY	0.98	2.19×10^{-4}
	Vertical ZY	0.98	2.45×10^{-4}
	Horizontal XZ	0.99	2.24×10^{-4}

Fractal dimension

The fractal dimensions showed no obvious differences among prey availability conditions (Table 3). However, D_f values suggested the existence of an anisotropy. In fact, without prey, the horizontal projections of larval paths were less convoluted than the vertical ones, implying an enhanced activity on the vertical axis. When prey were added, swimming complexity was similar in both projections, showing that larvae intended to explore all of the available space in a similar way.

Table. 3. **Fractal dimensions of the larval paths in both prey conditions.**

Prey condition	D_f of the vertical projection XY	D_f of the vertical projection ZY	D_f of the horizontal projection XZ
Without prey	1.62	1.61	1.53
	$R^2 = 0.99$	$R^2 = 0.99$	$R^2 = 0.99$
With prey	1.60	1.58	1.56
	$R^2 = 0.99$	$R^2 = 0.99$	$R^2 = 0.99$

Moment function of the displacements

The scaling of the norm $< \|\Delta X_\tau\|^q >$ vs. τ showed a good fit for at least 1.5 decades corresponding to time increments ranging from 0.1 to 5 s (Fig. 4 and Fig. 5). This good scaling supports the reliability of the behaviors of the function $\zeta(q)$ vs. q in both the absence and the presence of prey (Fig. 6).

The obtained $\zeta(q)$ function was non-linear for both prey conditions and for all projections. This reveals the multifractal nature of the larval paths (Fig. 6). Practically, this implies that the successive steps of the swimming of fish larvae were not random but self-correlated (*i.e.* existence of "memory"), and that large displacements were more frequent than what would be observed in a random walk.

There were differences in the scaling of $\zeta(q)$ depending on prey availability. In fact, the non-linearity of the $\zeta(q)$ function was more pronounced in the absence of prey (Fig. 6 A, B and C). However, this behavior was not observed in the horizontal (XZ) projection, on which prey availability did not affect the walk type (Fig. 6 D).

3.4 Discussion

A large body of literature revealed the patchy nature of plankton distribution in the ocean (*e.g.* Owen, 1989; Curry *et al.*, 1998). When prey densities outside patches are lower than those necessary to support growth, preying on a food patch is beneficial to larval fish (Peck and Daewel, 2007). An adequate search strategy is therefore needed to maximize the encounter of food clumps. Fine scale field observations showed that prey patches distribution is not normal (do not follow a Poisson distribution) (Young *et al.*, 2009) and that local food maxima are

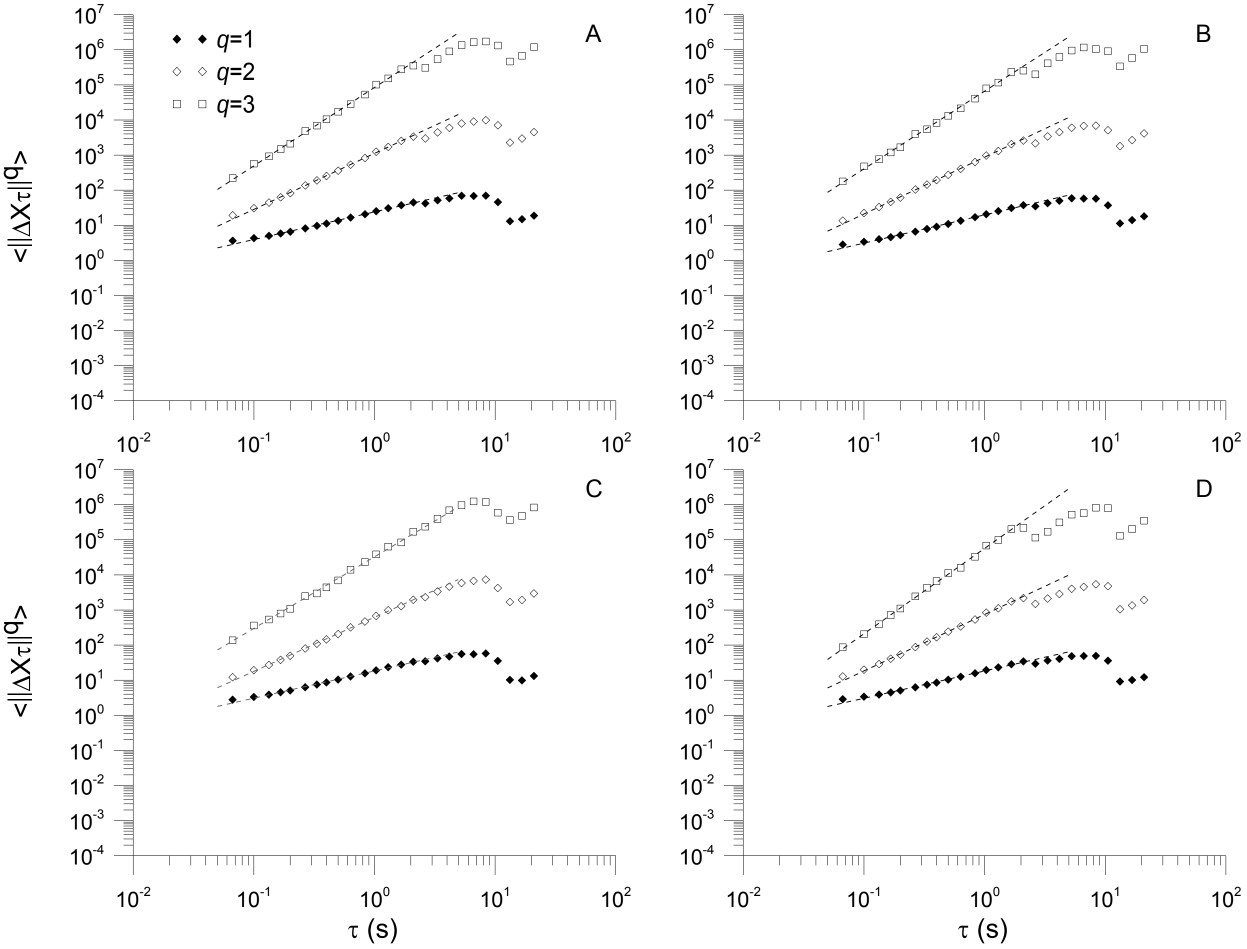

Fig. 4. Scaling of the norm $< \|\Delta X_\tau\|^q >$ vs. τ for q = 1, 2 and 3 of the displacements of *E. malabaricus* in 3D (A) on the vertical projection XY (B), the vertical projection ZY (C) and the horizontal projection XZ (D) in absence of prey.

generally horizontally distributed (Haury and Wiebe, 1982; Gallager *et al.*, 2004). A forager with enhanced vertical motion is therefore more likely to increase prey encounter probabilities (Fiedler, 1983; Jenkins, 1988). Our data showed that, in absence of prey, *E. malabaricus* larvae performed an extensive anisotropic search characterized by high amplitude vertical movements. This vertical swimming is consistent with an extensive foraging strategy adapted to horizontally distributed prey patches contrasting with the isotropic, intensive and area-restricted search pattern observed as prey were present. The shift from an extensive search to an intensive search

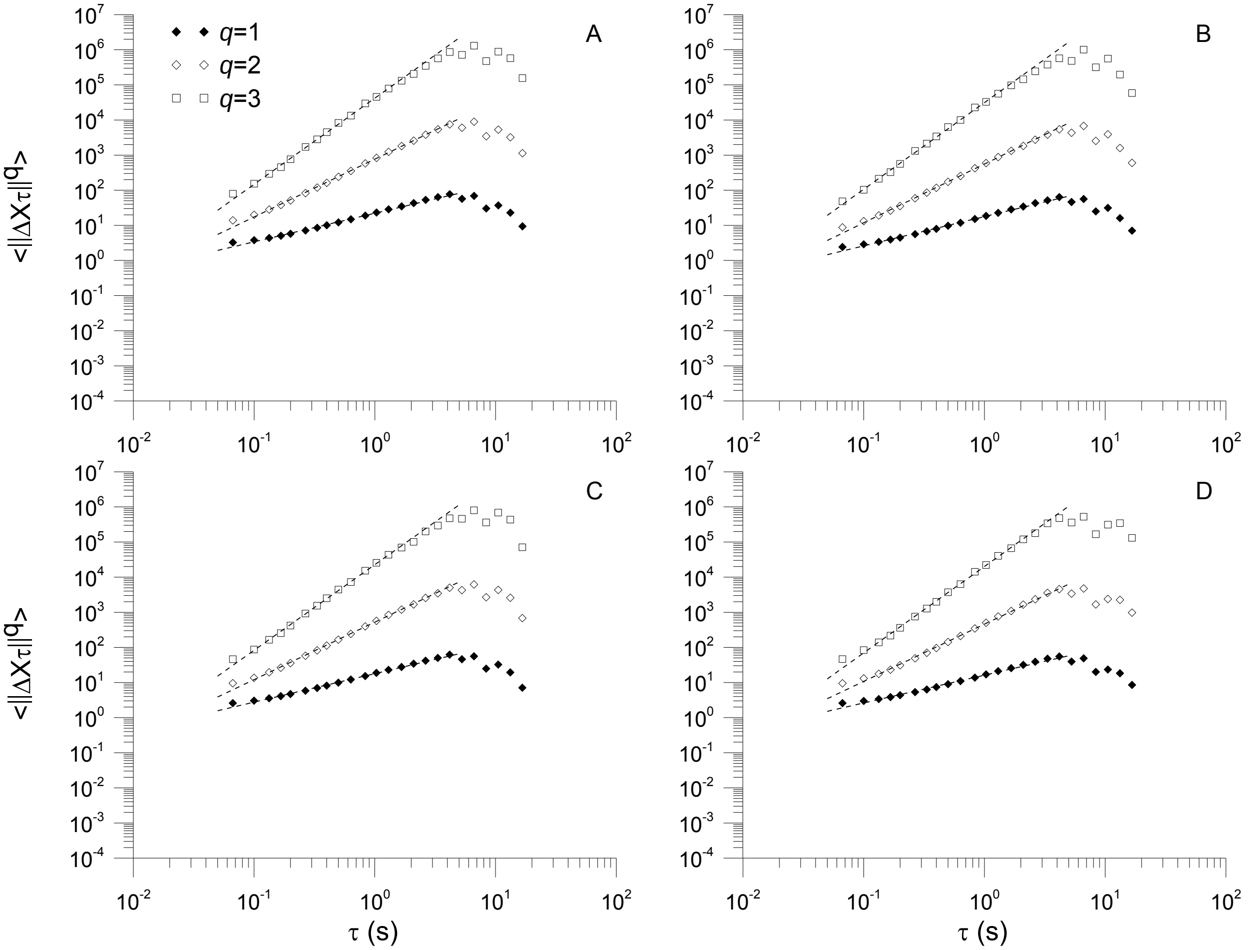

Fig. 5. Scaling of the norm $< \|\Delta X_\tau\|^q >$ vs. τ for q = 1, 2 and 3 of the displacements of *E. malabaricus* in 3D (A) on the vertical projection XY (B), the vertical projection ZY (C) and the horizontal projection XZ (D) in presence of prey.

when food patches are encountered is widespread behavior in the plankton. In fact, various plankters, like copepods (Tiselius, 1992; Bundy *et al.*, 1993), krill (Price, 1989) and fish larvae (Hill *et al.*, 2005) have been documented to decrease their motility when food is encountered in order to stay inside prey patches. In the case of *E. malabaricus* larvae, this behavior was associated with a decrease in the swimming speed on the vertical plane. Similar behavior was observed by Munk and Kiørboe (1985) and Munk (1995) for herring and cod larvae, respectively.

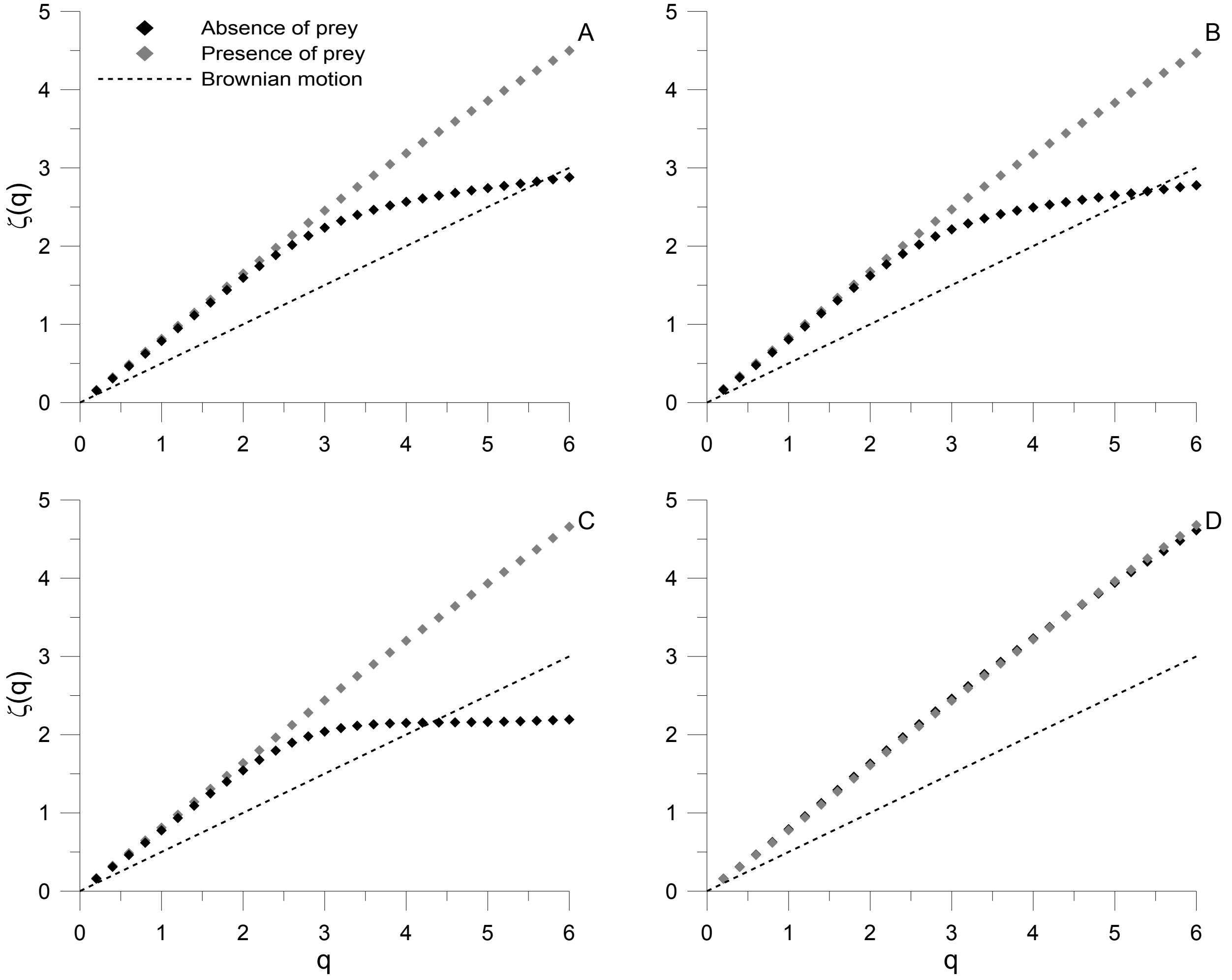

Fig. 6. **Scaling of moment exponents *ζ(q)* for the displacements of *E. malabaricus* in 3D (A) on the vertical projection XY (B), on the vertical projection ZY (C) and on the horizontal projection XZ (D). The function *ζ(q) = q/2* (Brownian motion) is shown in dotted line for comparison.**

Three advantages can be cited in order to explain this behavior. First, in presence of prey, decreasing swimming speed is beneficial for the energetic budget level since maintaining high speeds is costly (Hunt von Herbing *et al.*, 2001; Ruzicka and Gallager, 2006). Second, since speed governs the encounter rate (Gerritsen and Strickler, 1977; Visser, 2007) decreasing speed will also decrease the risk of encountering a predator. Finally, while a plankter conspicuousness is positively correlated with its velocity (Svensen and Kiørboe, 2000), swimming slowly will reduce the chances of being perceived by predators in vicinity. The investigation of the NGDR, used as a proxy for turning rates following Coughlin *et al.* (1992), showed that swimming paths were more convoluted when prey was absent. The motivation from this behavior is most likely to enhance encounters. In fact, it has been demonstrated that more complex paths maximize encounters when food is patchy (Coughlin *et al.*, 1992; Uttieri *et al.*, 2007; Cianelli *et al.*, 2009).

Fuiman and Webb (1988) reported swimming complexity to be proportional to *Re* for zebra fish larvae. Coughlin *et al.* (1992) further suggested that path complexity and swimming speed were linked parameters. Our results corroborate these hypotheses. In fact, the observed decrease in the swimming speed between both prey conditions resulted in a substantial decrease in *Re* and path complexity. The rationale is that enhanced speed increases *Re* and thus hampers the viscosity effects allowing more movement freedom to the fish.

Swimming paths of grouper larvae had a multifractal nature irrespective of prey availability. In a general framework where predators tend to optimize their search activity by adjusting it to the distribution pattern of their prey (Bartumeus *et al.*, 2003; Sims *et al.*, 2008), we hypothesize that the observed behavior is a response to the distribution pattern of prey in the ocean. In fact, zooplankters have a multifractal distribution in the ocean (Pascual *et al.*, 1995; Seuront and Lagadeuc, 2001). When first addressing the multifractal distribution of zooplankton, Pascual *et al.* (1995) rose up the lack of knowledge on the underlying mechanisms beyond to this pattern. We suggest the multifractal properties of the displacements reported from various zooplankters like copepods (Schmitt and Seuront, 2001; 2002), *Daphnia* (Seuront *et al.*, 2004b) and fish larvae (this study) to be one of the mechanisms leading to a multifractal distribution pattern in the natural environment. In spite of the uniformity of the walk type (*i.e.* multifractal in both absence and presence of prey) in larval grouper, the scaling of the moment function $\zeta(q)$ was influenced by the presence of prey. Indeed, when food was added, shorter displacements were more frequent which is consistent with an intensive search oriented toward smaller volumes. When food was absent, we observed a clear anisotropy characterized by more frequent long displacement on the vertical axis when compared to what was observed on the horizontal axis. Kiørboe (2008) reported an enhancement in the amplitude of the displacements of the copepod *Pseudocalanus elongatus* as food was removed and implied that such behavior will increase the chances of encountering a food patch. The anisotropic extensive search behavior observed for grouper larvae, further suggests that the variation of the motility patterns could also be adapted to the horizontal distribution of food patches in the natural environment.

Many theoretical works modeled the predator-prey encounters in both calm (Gerritsen and Strickler, 1977) and turbulent environments (Rothschild and Osborn, 1988; Lewis and Pedley, 2000). Most of these models implicitly assumed that predator search behavior is isotropic regardless of prey availability. Recently, Cianelli *et al.* (2009) addressed the effect of the predator walk type on the encounters in a patchy prey distribution. These authors showed that prey patchiness increases the variance of encounters (Cianelli *et al.*, 2009). While our results for fish larvae and those of Seuront *et al.*, (2004b) for other zooplankters show clear anisotropy in the swimming trajectories, modelling exercises do very rarely take into account this search behavior. More generally, our results show that 3D analyses alone can hide anisotropy. We therefore draw the attention of experimentalists to the usefulness of considering both vertical and/or horizontal projections, rather than the 3D, while designing experiments and analyzing data.

Finally, our results from the different analyses were complementary and pinpointed the fact that there is no single analysis allowing the detection of all behavioral patterns while investigating plankter's search mechanisms. Experimentalists should therefore choose the appropriate describers according to their objectives.

Chapter 4. Swimming behavior and capture success in European whitefish (*Coregonus lavaretus*) larvae on zooplanktonic prey[3]

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[3] From: MAHJOUB M.-S., O. ANNEVILLE, J. C. MOLINERO, S. SOUISSI and J.-S. HWANG, 2008. Feeding mechanism and capture success of European whitefish (*Coregonus lavaretus* L.) larvae. Knowledge and Management of Aquatic Ecosystems **388**: 1-14.

4.1 Introduction

The recruitment of pelagic fish species with high reproductive potential is highly variable, irrespective of marine (Koutsikopoulos and Le Cann, 1996) or fresh water species (Müller, 1992; Karjalainen *et al.*, 2000). Successful recruitment relies on adult spawning stocks (Helminen *et al.*, 1997), physical factors (Sirois and Dodson, 2000; Munk, 2007) and the availability of appropriate zooplankton prey (Rao, 2003). In addition, the accessibility of food not only depends on the relative prey abundance, but also on the predator's feeding adaptations (Pasternak *et al.*, 2006). An increasing research effort has been devoted to understanding the foraging behavior of fish larvae. Numerous aspects of predatory sequences like encounter rate (Mackenzie and Kiørboe, 1995), catch success (Drost, 1987; Domínguez-Domínguez *et al.*, 2002; Sarma *et al.*, 2003; Morales-Ventura *et al.*, 2004), attack success (Wanzenböck, 1992; Mackenzie and Kiørboe, 2000), and ingestion rate (Landry *et al.*, 1995) have been investigated. Previous studies also investigated the role of feeding mechanisms in the attack success of fish larvae and attributed the success of strikes to: i) the aptitude of the creation of a suction flow in larval carp (Drost and Van Den Boogaart, 1986) and larval clownfish (Coughlin, 1994), ii) the accuracy of larva and its strike speed in carp and pike larvae (Drost and Van Den Boogaart, 1986; Drost, 1987), iii) the duration of the fixation in cyprinids (Wanzenböck, 1992) and iv) the capability of larvae to approach a prey without eliciting an escape response in larval cod (Mackenzie and Kiørboe, 2000). A clear outcome of these investigations is that capture success constraints are species specific.

Common whitefish (*Coregonus lavaretus* Linnaeus, 1758) is an endemic planktivorous salmonid, constituting a major component of western European inland commercial fisheries (Marttunen and Vehanen, 2004; Gerdeaux *et al.*, 2006). In Lake Geneva, the increase of whitefish catches is partly due to the change of stocking practices from only yolk-sac fry to yolk-sac fry, juveniles (< 3 cm) and fingerlings (5-6 cm) (Gerdeaux, 2004). For this genus, in which the highest pre-recruitment mortality occurs during the larval stage (Karjalainen *et al.*, 2000), little is known about the factors governing the catch success and the survival of its larval stages.

Although many studies have identified several mechanisms involved in the capture success of fish larvae, less attention has been paid to the role of the larvae's path complexity. The aim of this study was to explore the mechanisms acting on the feeding success of larvae of *C. lavaretus*, which accounts for a substantial proportion of the total catches of Lake Geneva's fishery (Gerdeaux, 2004). To survey these mechanisms, we used standard cinematographic techniques and analyses of both scale dependent (distances and speeds) and scale independent (fractal dimension) metrics.

4.2 Material and methods

4.2.1 Experimental fish larvae and prey

Wild whitefish larvae were caught in the deep peri-alpine lake, Lake Annecy (28 km^2, maximum depth 65 m, France) in April 2006 using a rectangular net (1.5:1 m) of 5 m length (1 mm mesh). The cod end of this net was equipped with a PVC receiver to collect the larvae. Trawls of 20 min were performed at an approximate speed of 1 knot. Larvae were kept in an aquarium and fed on wild zooplankton for one day before the experiment. The day of sampling, mean water temperature was of 12 °C.

Reared larvae were obtained after the artificial fertilization of eggs produced from a broodstock originating from the Lake Geneva (582 km^2, maximum depth 309 m, France and Switzerland). When larvae emerged from the eggs, they were transferred in 1000 L tanks (density of 200-400 larvae L^{-1}) filled with lake water. In rearing tanks, larvae were fed on dry food pellets (INVE, 100–200 µm) and wild zooplankton.

The zooplanktonic prey used in our experiments were directly collected from the littoral zone of Lake Geneva. Water was filtered through a 200 µm mesh net and only organisms retained in the sieve were used as food. The biggest prey was *Daphnia* sp. (total length range: 0.45-1.75 mm).

4.2.2 Experimental setup

The animals were filmed in a small plexiglas tank of 10 × 8 × 3 cm (Length × Heigth × Depth) containing 0.24 L of filtred lake water. This experimental volume is insufficient to precisely determine the swimming patterns of whitefish larvae in the natural environment. Yet previous observations revealed that it allows whole predator-prey interactions events (from encounter to ingestion) to occur (Anneville *et al.*, unpublished data). It is therefore suitable for our specific objective of comparing successful versus failed capture events.

The 2D video set-up consisted of a single camera (Sony DCR PC120E) orthogonally oriented to the largest walls of the tank. The only light source was a fiber optic light (Zeiss KL Schott 8V 20 W) placed at ~10 cm above the tank. The light intensity was 48.9 µmol s^{-1} cm^{-2}. Water temperature during experimentations ranged from 15 to 17 °C.

4.2.3 Experimental procedure

The experimental procedure aimed to investigate the role of the feeding mechanism of whitefish larvae on its capture success. We carried out two experiments using larvae, as predators, facing two different prey types and densities. The two experiments were performed using non-starved larvae. In fact, preliminary observations showed that feeding larvae had fecal pellets obtruding from the anus, suggesting that these larvae did not stop feeding once the gut was full.

In the first experiment, Exp1: 3 wild larvae (total lengths: 14.6, 12.6 and 14.0 mm, stages 1 and 2 according to the classification of Luczynski *et al.*, 1988) caught from Lake Annecy one day prior to the experiment, were put into the observation tank. A mixture of 500 individual zooplanktonic prey composed by cladocerans (Bosminids and the two Daphnids *Daphnia hyalina* and *D. galeata*) and copepods (*Cyclops prealpinus*, *C. vicinus* and *Eudiaptomus gracilis*) caught from Lake Geneva were then added (max total length: 1.75 mm).

In the second experiment, Exp2: 4 reared larvae (total lengths: 15.3, 15.9, 15.1 and 15.5 mm, stages 2 and 3) were put into the vessel and 100 gently sorted adult *Cyclops* spp. (dominated by *C. prealpinus*; total length range: 1.0-1.65 mm) were added.

For both experiments, experimental prey sizes were consistent with prey sizes ingested in the field by the corresponding developmental stages of *C. lavaretus* (Anneville *et al.*, 2007b). The chosen densities, higher than those reported from Lake Geneva and Lake Annecy (Anneville *et al.*, 2007a; 2010), were intended to maximize predator-prey interactions. In both experiments predators and prey were first acclimatized during 10 min in the observation tank. This duration was chosen on the basis of pilot experimentations that revealed that this acclimatization period was sufficient to allow “normal” foraging behavior (Anneville, pers. comm.). Afterwards the larval behavior was recorded for 50 min.

4.2.4 Determination of swimming paths

A preliminary examination of the video recordings was performed in order to inspect the feeding patterns of whitefish larvae and to identify the preliminary set of predatory sequences (strikes, captures and escapes) to be analyzed. This analysis was conducted using the image processing software TrackIt V.2.0 (Net Tech Consulting, Iguana Gurus). This software permitted us to route zooplankters frame by frame at a time resolution Δt of 0.04 s. The coordinates of a larva corresponded to the position of the center of its eye (Mackenzie and Kiørboe, 2000), whereas the coordinates of a prey corresponded to the position of the center of its body. Each sequence resulted in a data base containing the spatial coordinates of each tracked zooplankter over time (x_i, y_i, t_i).

4.2.5 Behavioral parameters

The following metrics were considered in this study: The apparent predator attack speed (*AS*), the apparent prey escape speed (*ES*), the apparent fixation distance (*FD*), and the complexity of all trajectories during pursuit and attack phases using fractal dimension D_f. For Exp1, it was difficult to identify the prey type corresponding to each predator-prey interaction. In order to avoid errors in prey identification, data of Exp1 was pooled irrespective of prey species. We defined the investigated parameters as follows:

- Pursuit is the approach of the predator in the direction of a prey. As emphasized by Mackenzie and Kiørboe (2000) the pursuit can comprise repeated approaches if the prey exhibits escape drills. The fixation occurs during this event (Wanzenböck, 1992; Mackenzie and Kiørboe, 2000) and is defined as the disruption of the approach and the aiming at the prey (Wanzenböck, 1992). Georgalas *et al.* (2007) considered the “S” shaped posture as an independent event. However, we will associate this posture with the aiming since this lineament did not accompany all the predatory sequences.

- Attack (*A*) is the sudden strike of the larva toward a prey to engulf it (Heath, 1993).

- Success (C) is the capture of a prey by a larva and failure is the escape of a prey from its predator. The capture success (CS) is the number of successes divided by the total number of attacks:

$$CS = \frac{C}{A} \tag{10}$$

CS values range from 0 to 1 as attack efficiency increases.

- The instantaneous 2D swimming speed (V_{i2D}) of an event is estimated following the formula 4 (see chapter 3) with a time step $\Delta t = 0.04$.

- The predator attack speed (AS), is the apparent speed of the snap of the predator. It was calculated between the frame where the larva showed the first sign of the snap launch and the frame where the larva reached the initial position of the prey.

- The prey escape speed (ES), is the apparent speed of the first jump exhibited by a prey in response to a larval attack. This escape, if performed, could be achieved by one or more jumps. It was calculated between the frame where the prey showed the first sign of an escape reaction and the frame where the prey stopped its movement. When a prey did not perform any escape reaction, we assumed that $ES = 0$.

- The apparent fixation distance (FD), is the distance separating the predator from its prey during the aiming process. It was measured between the centre of the prey and the position of the larva on the frame preceding the strike.

- The fractal dimension (D_f) was based on the formula 6 (see chapter 3). In order to compare the complexity of predator paths between successful and failed attacks we pooled all individual trajectories for each situation. Then a single fractal dimension corresponding to all trajectories was computed for each situation.

4.2.6 Data analysis

The non-parametric Spearman Correlation Test was used to test for relationships between the following behavioral parameters: predator attack speed (*AS*), prey escape speed (*ES*), and fixation distance (*FD*). Wilcoxon Rank Sum test was used to compare behavioral variables between successful and failed strikes. All of these analyses and the estimations of the fractal dimension were performed using the MatLab software (7.5, The Math Works, inc.). Comparisons of the D_f for failed versus successful events was made by comparing the slopes of the linear fit of the log-log plot of $N(\lambda)$ versus λ.

4.3 Results

A total of 47 and 45 events were analyzed for Exp1 (wild larvae) and Exp2 (reared larvae), respectively.

4.3.1 Feeding ethogram and kinematics

The accurate analysis of all video recordings (*i.e.* sequence by sequence and frame by frame when necessary) allowed us to describe the successful predatory sequence of *Coregonus lavaretus* larvae as follows: search, encounter, pursuit, attack, capture and ingestion.

Whitefish larvae only detected prey during swimming and hence appeared to be a cruise predator. During pursuit, larvae swam backwards to reach an appropriate aiming distance from the prey in 31.91% of the events in Exp1 and 6.25% of the events in Exp2. This pattern was not observed for the remaining sequences. Afterwards, larvae fixated the prey by keeping their head immobile and by wiggling the posterior part of their body. Before the attack, an “S” shaped posture was exhibited in 44.66% of the attacks of wild larvae and 31.25% of the attacks of reared larvae. *C. lavaretus* larvae always fixated its prey from below and stroked a few mms towards it to simply engulf it. During the attack, no prey was caught up in a flow towards the predator; showing no cues for the creation of a suction current. The overall *CS* was 0.29 for Exp1 (wild larvae) and 0.46 for Exp2 (reared larvae). The mean predator attack speed projected on the vertical plane oscillated around 36 mm s^{-1} and the fixation distance was around 1.7 mm (Table 4).

Table. 4. Mean values (± s.d.) of the different events occurring during whitefish larva attacks. n: number of observations; *AS*: mean predator attack speed (mm s^{-1}); *ES*: mean prey escape speed (mm s^{-1}); *FD*: mean fixation distance (mm).

Experiment	n	*AS* mm s^{-1}	*ES* mm s^{-1}	*FD* mm	Capture Success ratio
Exp1 (wild larvae)	47	36.34 ± 14.39	26.45 ± 20.79	1.75 ± 0.71	0.29
Exp2 (reared larvae)	45	36.81 ± 25.80	15.97 ± 23.83	1.65 ± 0.76	0.46

The fixation distance (*FD*) was positively correlated with the larva attack speed (*AS*) for both Exp1 ($p < 0.001$, Table 5) and Exp2 ($p < 0.001$, Table 5). No correlation was found between prey escape speed (*ES*) and *FD* or between *ES* and AS in Exp1. In Exp2, both *FD* and *AS* were positively correlated with *ES*. This implies that the prey could adjust their escape speed to the attack speed of the larva.

Table. 5. Correlation coefficients and p values of Spearman correlation test for both experiments. n: number of observations; *AS*: mean predator attack speed; *ES*: mean prey escape speed; *FD*: mean fixation distance.

	Exp1 (wild larvae)			**Exp2 (reared larvae)**		
	R	n	p	R	n	p
FD* vs. *AS	0.50	47	< 0.001	0.76	45	< 0.001
FD* vs. *ES	0.28	47	0.05	0.43	45	0.003
AS* vs. *ES	0.21	47	0.17	0.60	45	<0.001

4.3.2 Comparison of successful vs. failed events

Comparisons of parameters for successful versus failed events revealed that escape speed (*ES*) and fixation distance (*FD*) were significantly lower during success than during failure.

Table. 6. Mean values (± s.d.) of the different events of whitefish larva attacks for successful and failed attacks and p value of Wilcoxon test for both experiments. n: number of observations; *AS*: mean predator attack speed (mm s^{-1}); *ES*: mean prey escape speed (mm s^{-1}); *FD*: mean fixation distance (mm).

Predator origin		**n**	***AS***	***ES***	***FD***
Exp1	Success	14	32.12 ± 16.03	1.14 ± 3.42	1.41 ± 0.44
(wild larvae)	Failure	33	37.90 ± 13.92	37.19 ± 14.75	1.90 ± 0.76
	p value	-	0.173	<0.001	0.012
Exp2	Success	21	28.41 ± 18.58	1.36 ± 3.13	1.35 ± 0.55
(reared larvae)	Failure	24	44.15 ± 29.20	28.68 ± 26.66	1.91 ± 0.84
	p value	-	0.078	0.002	0.007

4.3.2.1 Attack speed (AS)

The mean attack speeds of larvae were lower for successful snaps compared with failed snaps. However, these differences were not significant for Exp1 or for Exp2 (Table 6).

4.3.2.2 Escape speed (ES)

The mean escape speeds of prey were significantly lower in successful than in failed attacks for both Exp1 (Wilcoxon Rank Sum Test, $n = 47$, $p < 0.001$, Table 6) and Exp2 (Wilcoxon, $n = 45$, $p < 0.01$, Table 6). Nevertheless, an escape response was performed by only 14.28% of captured prey in Exp1 and 15.38% in Exp2.

4.3.2.3 Fixation distance (FD)

The fixation distance was shorter in successful attacks compared with failed attacks. This trend was significant for both Exp1 (Wilcoxon, n = 44, $p < 0.05$, Table 6) and Exp2 (n = 45, $p < 0.01$, Table 6).

4.3.2.4 Fractal dimension (D_f)

The log-log plots of $N(\lambda)$ against λ were strongly correlated to the linear fit ($R^2 = 0.99$) for both experiments (Fig. 7). The path complexity of successful events was lower than path complexity of failed events for both experiments. In fact, the fractal dimensions for successful events were lower than those for failed events (Table 7). This implies, as we will clarify later, that a convoluted pursuit was less likely to result in a successful event.

Table. 7. Fractal dimensions (D_f) for successful and failed attacks for whitefish larvae (Exp1: wild larvae and Exp2: reared larvae) obtained for all trajectories. Confidence intervals (CI) correspond to fractal dimension estimates at 95%.

Predator origin		**n**	D_f	**CI**	R^2
Exp1	Success	14	1.24	[1.22-1.27]	0.99
(wild larvae)	Failure	18	1.37	[1.34-1.40]	0.99
Exp2	Success	12	1.25	[1.22-1.28]	0.99
(reared larvae)	Failure	18	1.33	[1.30-1.35]	0.99

4.4 Discussion

4.4.1 Feeding mechanism

An accurate portrayal of fish larvae's searching mechanisms facilitates the investigation of predator-prey interactions and provides insight into larval foraging efficiency (Browman and O'Brien, 1992). The analysis of the foraging behavior of common whitefish larvae in this study showed that these predators have the ability to locate prey while moving. We can accordingly classify their behavior as cruise predators, like herring (Munk and Kiørboe, 1985) and clownfish (Coughlin, 1993) larvae. Coughlin (1993) hypothesized that the prey location space for this type of predator could better be explained as a probability space rather than the boundary of the visual capabilities previously suggested by Browman and O'Brien (1992). The probability space is a succession of probability areas with the closest one being the one where the prey location probability reaches its maximum (Coughlin, 1993). The ability of a larval fish to detect a prey directly at the front of its head depends on the existence of an overlap of the visual fields of its two eyes (Coughlin, 1993). While analyzing the pursuit sequences of whitefish larvae, we observed that these larvae seldom swam backward while orienting toward the prey before aiming at it (31.91% for Exp1 and 6.25% for Exp2). This result might suggest the existence of a limited perception area just in front of the snout of this larval species. Support for this hypothesis is given by the absence of binocular vision in larval fishes from the Coregoninae subfamily (Braum, 1978).

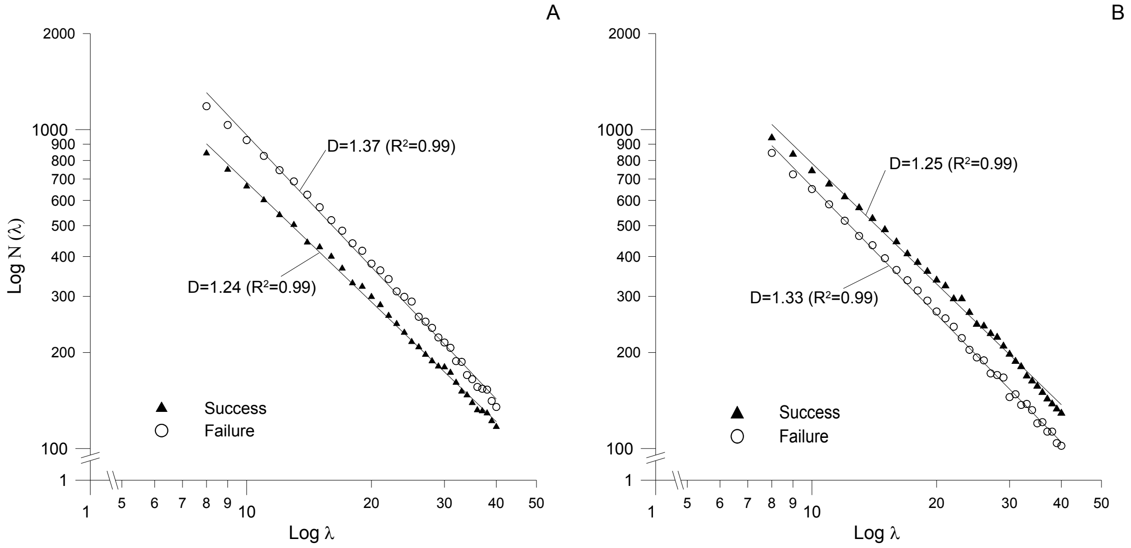

Fig. 7. Scaling of the log–log plots of *N(λ)* versus *λ*. (A) for Exp1 (wild larvae) and (B) for Exp2 (reared larvae).

Blueback herring (*Alosa aestivalis*) and herring (*Clupea harengus*) have been shown to mostly attack their prey from below (Janssen, 1981; Thetmeyer and Kils, 1995). Coughlin (1993) also reported that clownfish larvae detected more prey items in the upper half of their perception field. Our results, showing that *C. lavaretus* larvae always aimed and attacked their prey from below, suggest that whitefish larvae have developed the same foraging mechanisms as these planktivorous predators. One should expect that efficient planktonic foragers have evolved toward mechanisms allowing them to detect prey items without being seen. Previous studies which investigated the benefits of searching and attacking the prey from below discerned different advantages for this strategy. On the one hand, planktonic organisms have higher contrast with the background and are more conspicuous when observed from below (Thetmeyer and Kils, 1995), especially when they are located outside the Snell's window (Janssen, 1981). On the other hand, the predator is hidden to its target prey when located below it (Thetmeyer and Kils, 1995). Finally, approaching from below could be a strategy of the predator to avoid casting a shadow that might warn the prey. In fact, rapid decreases in light intensity are known to trigger escape responses in copepods (Buskey and Hartline, 2003).

The results obtained in both Exp1 (0.29) and Exp2 (0.46) suggest that *C. lavaretus* larvae have a relatively low capture success rate. Even prey to predator size ratios were higher (0.01-0.13 for wild larvae and 0.06-0.10 for reared larvae) than an optimal ratio of 0.01 (Heath, 1993), we remind that prey sizes used here are those faced by *C. lavaretus* in the natural habitat. Low capture success ranging from 0.03 to 0.21 were also reported for early larval stages of other species of the genus *Coregonus* fed on mixed zooplankton (Braum, 1963). Indeed, when a larval fish shifts to external feeding it has not yet fully developed optimal feeding abilities and its capture success could therefore be low (Rao, 2003).

4.4.2 Feeding kinematics

The positive correlation between the *AS* and the *FD* for both Exp1 and Exp2 could represent a strategy used by the predator to overcome the drawbacks of a longer attack distance associated with an increased risk of being detected. Only Exp2 showed significant correlations between *FD* and *ES*, in fact for Exp1 the positive trend was weak ($p = 0.052$). However, it is worth noting that the fixation distance and the escape presumably occur on different planes, whereas our estimations, which are only projections on the vertical plane, underestimate the distances and speeds. As a general trend, although not statistically confirmed for Exp1, these results point toward that farther attacks are associated with faster escape responses of prey. Hydromechanical perception of predators in copepods has been widely documented (Yen and Strickler, 1996; Kiørboe and Visser, 1999; Kiørboe *et al.*, 1999; Hwang and Strickler, 2001; Wagget and Buskey, 2007). It is also known that copepods can sense faster predators at a longer distance (Viitasalo *et al.*, 1998) and can adjust their escape response to the intensity of the mechanical stimuli (Heuch *et al.*, 2007). The positive correlation between attack speed and prey escape speed for reared whitefish larvae in this study supports these hypotheses and shows that the faster the larva, the faster the escape response.

We admit here the existence of a trade-off between the advantages of enhancing the attack speed (so as to decrease the attack duration and hence the risk of being perceived) and the disadvantages of diminishing it (in order to encompass the escape response of the prey). Accordingly, a successful snap should be quick enough to catch the prey off guard but not too fast in order to avoid eliciting an escape response. This balance can be achieved when the predator attacks on its prey from a closer distance (*i.e.* short fixation distance).

4.4.3 Factors governing the capture success

Differences in the predatory behavior were found between failed and successful attacks in both Exp1 and Exp2. Comparison of the kinematics of failed versus successful attacks showed that successful events were characterized by a minor prey escape speed. We should note here, however, that only about 15% of captured prey elicited an escape response before being captured. This suggests that the fate of the prey probably depends on its ability to detect the predator rather than its ability to perform a successful escape response once detected. As a result, the attack success of whitefish larva seems to be determined by events occurring upstream of the attack.

Viitasalo *et al.*, (1998) and Mackenzie and Kiørboe (2000) attributed the capture success of fish larva to the ability of the predator to get within a attack distance close enough to the prey without triggering an escape response. This observation was tested and confirmed by a mechanistic modelling approach (Caparroy *et al.*, 2000) as well as an empirical observation (Hunt von Herbing and Gallager, 2000). Our results, showing significantly higher fixation distances for failed attacks compared to successful attacks, corroborate the results of the above cited authors.

It has been documented that planktonic organisms may vary their path complexity in order to enhance their encounter rates (Coughlin *et al.*, 1992; Uttieri *et al.*, 2007a). The results of a simulation exercise comparing different search strategies by Uttieri *et al.* (2007b) implied that high fractal dimensions are more advantageous at high food concentrations, whereas less convoluted trails are sufficient when food is scarce. In this hypothesis an implicit assumption is that the escape performances of prey are comparable for all search strategies irrespective of the search and/or pursuit’s complexity. Although numerous studies on the mechanoreception capabilities of planktonic prey have been reported (Hwang and Strickler, 1994; Fields and Yen, 1997; Hwang and Strickler, 2001; Burdick *et al.*, 2007), it remains unclear whether the complexity of the swimming path of a predator can influence the escape response of the prey. The present study supports that the contortion of the swimming path of European whitefish larvae is of primary importance to its capture success. In fact, for both of our experiments using wild larvae and reared larvae, low fractal dimensions values D_f were associated with success whereas high values of D_f were associated with failed events.

4.4.4 Limitations of the approach and data

In our experiments, we recorded the projection of predator and prey paths on the vertical plane. Accordingly, all the distances and speed values of events not aligned parallel to the camera view were underestimated. To reduce such biases, Mackenzie and Kiørboe (2000) multiplied the average 2D distances and velocities by 1.225 to obtain 3D estimates. However, the shape of our experimental vessel, being 3 times larger than deeper, was designed to maximize the occurrence of events on planes not far from orthogonal to the cameras axis and thus, to reduce the 2D biases.

As highlighted by Seuront *et al.* (2004a), most frequently used metrics in behavioral ecology are scale dependent. In other words we obtain a different value each time we change the time resolution. Keeping in mind that there is no particular scale at which these metrics can be precisely estimated (Seuront *et al.*, 2004a), we decided to contrast metrics of failed versus successful attacks, rather than trying to accuratly estimate them.

While acknowledging the limitations of the approach and data provided by our experiments, we consider the video recording approach to be a useful tool that can provide insight into the mechanisms acting at the individual scale. We want to emphasize that the results provided by our experiments can be viewed in a simplified context (*i.e.* without turbulence) of whitefish larva – zooplankton interactions. Further research is therefore necessary to assess the mechanisms highlighted in this study at different levels of turbulence using different prey types and a three-dimensional video imaging technique to test for behavioral isotropy.

Our study relied on both wild and reared larvae, which constitute the two components of the whitefish larvae stock in Lake Geneva. Although no direct comparison was made between the two groups, we could find no differences in the parameters involved in the capture success (*i.e.* fixation distance and path complexity) of whitefish larvae. These results may serve as basis for further investigations required to elucidate the factors governing the feeding success of *C. larvaretus* larvae. Indeed, further works can be directed towards the reaction distance of planktonic prey available to whitefish larvae, and also the relationships between the swimming patterns of whitefish larvae and their prey. Such studies are needed to improve our knowledge of the feeding efficiency of whitefish larvae and may provide valuable tools to enhance the efficiency of commonly used techniques for artificial stocking of this species.

Chapter 5. Swimming kinematics of *Eurytemora affinis* (Copepoda, Calanoida) reproductive stages and differential vulnerability to predation of larval *Dicentrarchus labrax* (Teleostei, Perciformes)[4]

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[4] From: MAHJOUB M.-S., S. SOUISSI, F.G. MICHALEC, F. SCHMITT, and J.-S.HWANG, (*under revision*) Swimming kinematics of *Eurytemora affinis* (Copepoda, Calanoida) reproductive stages and differential vulnerability to predation of larval *Dicentrarchus labrax* (Teleostei, Perciformes). *Journal of Plankton Research*.

5.1 Introduction

The structuring role of fish predation on zooplankon communities has been largely documented (*e.g.* Lazzaro, 1987). In the natural environment, interactions occur at the individual level, rather than at the level of whole populations (Kiørboe, 2008). Investigating the predator-prey interactions at the individual level seems therefore essential for a better understanding of the ecosystem dynamics. In the megatidal Seine estuary (English Channel, France) the copepod *Eurytemora affinis* (Poppe, 1880) is one of the dominant mesozooplanktonic species (Devreker *et al.*, 2008). It has been reported to be one of the main food sources for larvae and 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 females of *E. affinis* were reported to be more vulnerable to predation than non-ovigerous females or males (Sandstrom, 1980; Vuorinen *et al.*, 1983). 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 also attributed to their bigger size and lower escape abilities (Svenson 1992, 1997a, 1997b). However, for *Eurytemora affinis* that inhabits the Seine estuary, where both high turbidity and low light penetration limit vision, the underlying mechanisms beyond the enhanced vulnerability of ovigerous females are yet to be investigated. In fact, *D. labrax*, one predator of *E. affinis* in the Seine estuary (Mouny *et al.*, 1998), presents a retina with a high concentration of rods (responsible for shape and movement detection) and large cones ensuring nocturnal vision by means of detection of a moving prey (Mani-Ponset *et al.*, 1993). In addition, nocturnal feeding has been reported for juveniles of *D. labrax* (*e.g.* Sánchez-Vázquez *et al.*, 1995). In a laboratory experiment, we tested for the ability of *D. labrax* larvae to feed on *E.*

affinis in darkness. Then, we assessed the relative vulnerability of the three reproductive stages (males and non-ovigerous females) of *E. affinis* to sea bass larvae in relation to their swimming behavior. Finally, we aimed at testing the hypotheses that higher vulnerability of a reproductive stage to predation is due to i) reduced escape ability, ii) larger body size, iii) differential swimming behaviors.

5.2 Material and methods

5.2.1 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 *et al.*, 2007). Individuals of this species show a sexual dimorphism marked by females (mean prosome length = 1003.3 µm) bigger than males (mean prosome length = 954.2 µm) (Souissi *et al.*, 2010). Using oblique tows of a WP2 net (200 µm) copepods were collected from the Seine estuary, near the Tancarville Bridge during ebb tide in October 2007. Samples 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 a salinity of 15 and a temperature of 18 °C. Salinity was thereafter progressively increased to 25 by gradually adding filtered sea water. Salinity of 25 was chosen in order to ensure a tradeoff between fish rearing salinity (32) and copepods' optimal salinity for a maximum distribution range in the Seine estuary (5-18) (Mouny and Dauvin, 2002; Devreker *et al.*, 2007). Copepods were fed daily on the red algae *Rhodomonas marina* during the three days preceding the experiments.

5.2.2 Experimental fish

The European Seabass (*Dicentrarchus labrax*) is a commercially important fish species that inhabits both marine and estuarine environments of European waters (Kelly, 1988). Larval stages of this fish start colonizing estuaries of English Channel during May-June (Kelly, 1988). Larvae, 47 days post hatching (TL = 19.4 ± 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 to a salinity of 25, fish larvae were kept in 30 L aquaria on a 16:8 (light:dark) cycle at a temperature of 18 °C. 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 devoid of food for the 24 h preceding the experiments.

5.2.3 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 of the motion of copepods and fish, we used a single infra-red sensitive Camera (DV Sony DCR, 25 Hz) which axis was placed horizontally in order to orthogonally face one vertical vessel wall.

In turbid estuarine waters, visible light is rapidly attenuated (Kirk, 1994a; 1994b) 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 copepods' phototropism, we performed our experiments under near infra-red illumination (darkness hereafter). Light-emitting diodes (LED, 880 nm; 0 lux) were placed below the experimental vessel and provided the only illumination source for the camera.

5.2.4 Experimental procedure

We sorted copepods according to their reproductive stage: males, non-ovigerous females (females hereafter) and ovigerous females. Before each experiment 145 copepod individuals were gently transferred into the filming vessel filled with 3.12 L of filtered water. We used a density of 43 ind. L^{-1} comparable to regularly recorded densities of adult *E. affinis* in the Seine estuary (Devreker, 2007; Devreker *et al.*, 2008). At the meanwhile, three fish larvae were placed in a separate 250 mL beaker. Copepods and fish were acclimatized to room light and temperature for 15 minutes. Subsequently, the larvae were added into the experimental vessel and the behavior of the animals was recorded during 30 minutes. For each prey treatment (males, females and ovigerous females) 4 replicates were performed yielding a total of 6 hours of video recordings. In total, we used 1740 copepods as prey and 36 fish larvae as predators. Experimental water temperature measured before and after each experiment ranged from 18 to 21 °C.

5.2.5 Video analyses

5.2.5.1 Predator behavior

We first proceeded to a visioning of all of the 6 hours of videos corresponding to the three treatments in order to identify and label the following predator behaviors:

Attack (*A*) (see chapter 4);

Capture (*C*) (see chapter 4);

Rejection (R): when a prey is rejected from the larva's mouth subsequently to a successful capture;

Ingestion (I): when no rejection occurs after a successful attack;

Capture success (CS) (see chapter 4).

Prey densities affect food intake levels (*e.g.* Milinski, 1977), a differential decrease in the number of prey among treatments would, therefore, result in different consumption rates (prey × fish^{-1} × time^{-1}). This will render the comparison of consumption rates among prey treatments questionable. Here, we only considered the prey vulnerability after the entire exposure duration (30 min) as mean numbers of ingested prey across prey treatments.

5.2.5.2 Prey behavior

The vertical projections of the swimming paths of copepods were digitized using the LabTrack software (Labtrack, 2.1, Bioras). Only 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 5.2×10^6 coordinates was obtained with 2163, 1643, and 1684 trajectories for males, females and ovigerous females, respectively. Parameters likely to affect the predator-prey interaction, copepod swimming speed (Blais and Maly, 1993; Kiørboe, 2008) and acceleration were compared among treatments.

5.2.5.3 Speed

Instantaneous speeds (V_{i2D}) were computed at the lowest time resolution (t = 0.04 s) following the formula 4 (chapter 3). In order to compare the swimming speeds across reproductive stages, we first averaged the instantaneous speeds for each trajectory (V_t) and then computed the mean speed for each reproductive state (V_{rs}).

5.2.5.4 *Acceleration*

Acceleration is an important quantity for zooplanktonic prey as they need to elicit rapid accelerations in order to escape predators. 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.* (2002) have recorded acceleration events as high as 255 m s^{-2} and 319 m s^{-2} for the copepods *Acartia tonsa* for *A. lilljeborgii*, respectively. In the present study, our video recording frequency of 25 Hz is unlikely to be high enough to resolve the true copepod accelerations. However, we can compare accelerations performed by the different reproductive stages measured at the same temporal scale.

Absolute values of instantaneous accelerations (A_{i2D}) were thereafter computed as follows:

$$A_{i2D} = \frac{\left|V_{(i+1)2D} - V_{i2D}\right|}{0.04} \qquad (11)$$

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

5.2.6 Statistical analyses

Comparisons of ingestions (I), capture successes (CS) and rejections (R) across treatments were conducted using the χ^2 test following McDonald (McDonald, 2009). Comparisons of the mean swimming speeds as well as the accelerations 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 the MatLab software (7.5, The Math Works, inc.).

5.3 Results

Dicentrarchus labrax larvae were able to detect, to attack and to feed on *E. affinis* in darkness. Sea bass larvae were pause-travel predators altering swimming bouts with pauses during which they detected prey items. Males, females and ovigerous females did not suffer the same mortality (Fig. 8, χ^2; $p < 0.01$). Ovigerous females suffered 75% and 63% higher mortality than males and females, respectively. Females underwent 32% higher predation than males. However, this difference was not statistically significant (χ^2; $p > 0.05$).

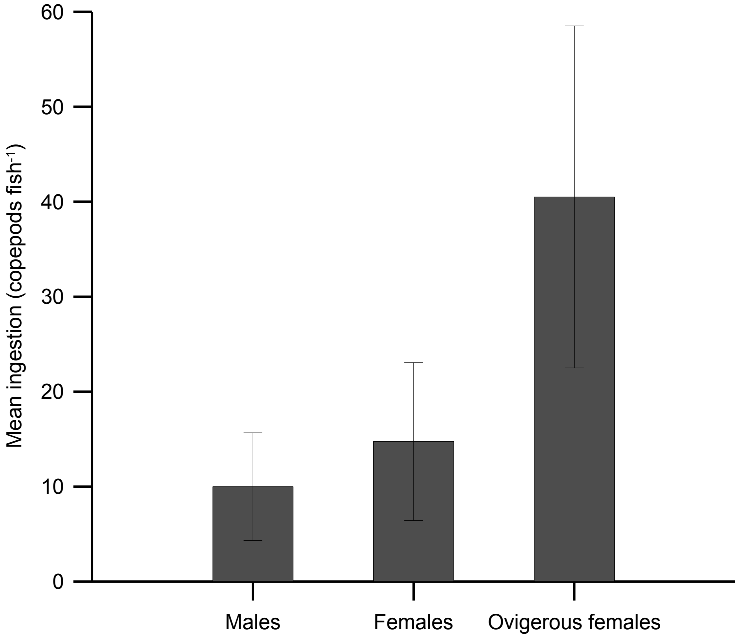

Fig. 8. Mean (± s.e.) ingested males, females and ovigerous females of the copepod *Eurytemora affinis* per *Dicentrarchus labrax* larvae.

No significant differences were detected in capture success (*CS*) across the treatments (Fig. 9, χ^2; $p > 0.05$). Likewise, rejections, which represented only 2.7% of the overall attacks, were not significantly different among the prey treatments (χ^2; $p > 0.05$).

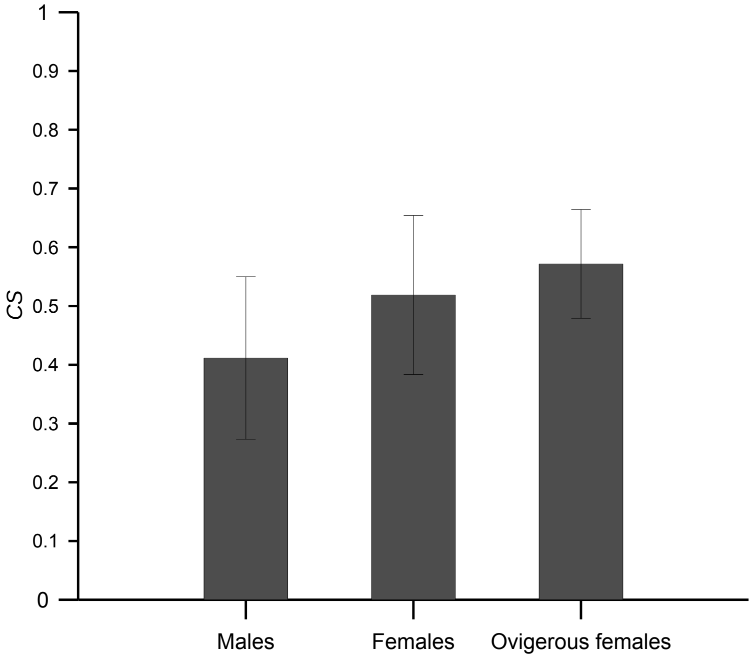

Fig. 9. Mean (± s.e.) capture success (*CS*) of *Dicentrarchus labrax* larvae on males, females and ovigerous females of the copepod *Eurytemora affinis.*

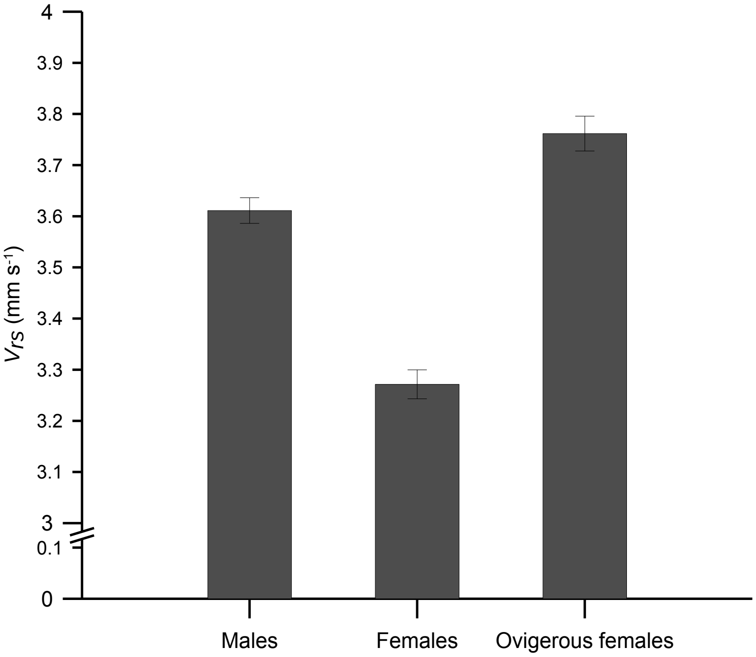

Fig. 10. Mean (± s.e.) speed (**V_{rs}**) for males, females and ovigerous females of the copepod *Eurytemora affinis* (n = 5454).

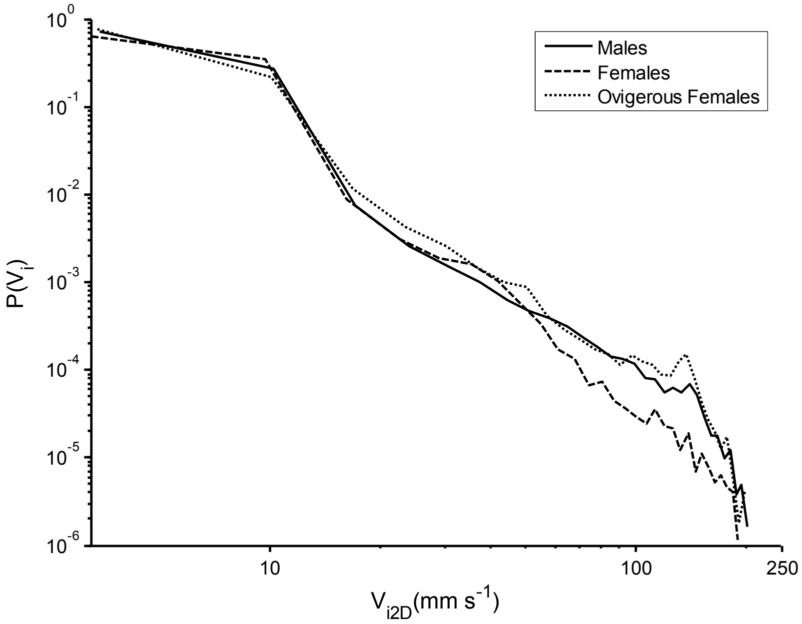

Fig. 11. **Probability density function of the instantaneous speeds (*V_{i2D}*) for males, females and ovigerous females of the copepod *Eurytemora affinis* (n = 5.2 x 10^6).**

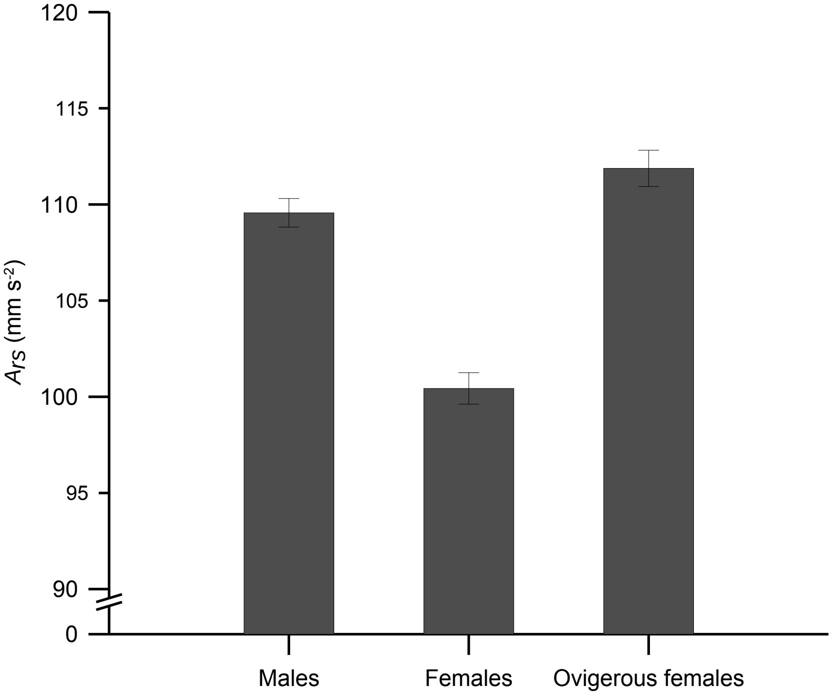

Fig. 12. **Mean (± s.e.) acceleration (*A_{rs}*) for males, females and ovigerous females of the copepod *Eurytemora affinis* (n = 5454).**

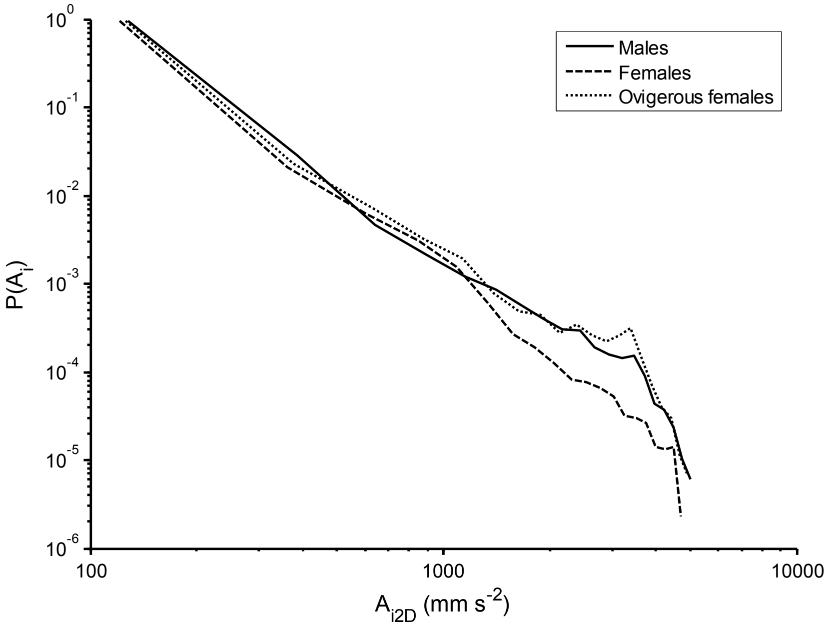

Fig. 13. Probability density function of the instantaneous acceleration (A_{i2D}) for males, females and ovigerous females of the copepod *Eurytemora affinis* (n = 5.2 x 10^6).

Mean swimming speeds (V_{rs}) were different across reproductive stages (Fig. 10; K-W, $p < 0.001$). In presence of predators, ovigerous females swam faster than males (Wilcoxon; $0.05 < p < 0.01$) which in turn swam faster than females (Wilcoxon; $p < 0.01$). This trend was corroborated by the Probability Density Function (*PDF*) distribution of instantaneous speeds (Fig. 11).The different reproductive stages of the copepod *E. affinis* displayed different mean accelerations (Fig. 12; K-W, $p < 0.001$). No differences could be detected between the mean accelerations of males (109.5 ± 34.6 mm s^{-2}) and ovigerous-females (111.8 ± 38.7 mm s^{-2}, Wilcoxon; $p > 0.05$). However, females had a significantly lower mean acceleration (100.4 ± 33.2 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 instantaneous accelerations (Fig. 13).

5.4 Discussion

5.4.1 Larval predation in darkness

While larval fish are usually acknowledged to be visual predators, larval striped bass *Morone saxatilis*, a confamiliar of European sea bass, has been reported to feed and grow in darkness when feeding on *E. affinis* (Chesney, 1989). Our study further reveals that larval stages of *D. labrax* are able to remotely locate, attack and capture the copepod *E. affinis* in darkness. In the present experiment, capture successes under near infra-red light were lower than the values of 0.5 to 0.65 observed for the same fish under light conditions (our own unpublished data). These relatively low capture successes may also be explained by a relatively high prey to predator size ratio of 0.05 compared to an optimal ratio of 0.02 for comparable size herring larvae feeding on copepods (Munk, 1992). Remote detection in fish may be achieved through chemoreception, vision and mechanoreception. While chemoreception has been proven to help fish larvae orient toward food patches (Tanaka *et al.*, 1991; Knutsen, 1992) there was no evidence that fish can discern an individual prey item among others solely relying on chemical cues. Accordingly, it is unlikely that *D. labrax* larvae relied on chemoreception to detect and attack prey items. In the present experiment, we rather suggest that fish mainly relied on vision and mechanoreception to spot the individuals of *E. affinis*. Moreover, our observations corroborated the results of Georgalas *et al.* (2007) and showed that *D. labrax* larvae are pause-travel predators, a strategy of species inhabiting environments with '*heterogeneous background*' (*e.g.* estuaries) intended to facilitate the detection of moving prey (Janssen, 1992). Finally, while the role of neuromasts in nocturnal feeding has been revealed for the larval stages of different fish species (Jones and Janssen, 1992; Mukai *et al.*, 1994), such structures have been proven to be functional as early as the larval phase in *D. labrax* (Diaz *et al.*, 2003), supporting the role of mechanoreception in the feeding of sea bass larvae.

5.4.2 Differential vulnerability of *E. affinis* reproductive stages

Higher vulnerability of ovigerous female copepods has already been reported for *Euchaeta elongata* (Bollens and Frost, 1991), *Eudiaptomus gracilis* (Svensson, 1992; Svensson, 1997a, 1997b; 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. Herein, we discuss three hypotheses which may 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 of sea bass larva 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 eggs, 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 females of *E. affinis* are able of more vigorous accelerations than either males or females, which has also been observed by Michalec *et al.* (2010) for copepods swimming in absence of predators. Moreover, the capture success of *D. labrax* larvae was not significantly different across *E. affinis* reproductive stages. 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. Because the numbers of rejections were similar among treatments, the higher vulnerability of ovigerous females should be attributed to events occurring before the pursuit. These events are the encounter and the decision of the predator to pursue the prey (Rao, 2003), which can be both triggered by the motility of the prey (Bengston, 2003; Buskey, 2005; Kiørboe, 2008). 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 *Eudiaptomus gracilis* (Svensson, 1997b), higher vulnerability of ovigerous females can be explained by their bigger size. In fact, it has already been shown that bigger planktonic prey are detected at farther distances from the predator than smaller prey (O'Brien, 1987). Moreover, females with larger egg clutches suffer higher predation than those with smaller egg sacs (Svensson, 1995). If size alone accounts for higher ingestion rates, then ovigerous females should suffer from higher mortality than females. In turn, females would suffer higher mortality than males. However, our results show no mortality difference between males and females, corroborating the results of Vuorinen *et al.* (1983) who found no differences in predation rates suffered by males and females of *Eurytemora hirundoides*, a synonym of *E. affinis* (Busch and Brenning, 1992). Though size alone does not explain to the observed differential mortality, it may act in synergy with another parameter. As a matter of fact, Kiørboe and Visser (1999) demonstrated that perception is not only dependent on prey size, but also on the prey velocity. 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. On the one hand, in estuarine areas with high densities of non-living suspended matter, prey movement patterns can be used to discriminate living prey form inert particles (Buskey *et al.*, 1993). On the other hand, 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 acceleration. Swimming speed of a prey is known to cause 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 (Visser, 1999; Kiørboe, 2008). In our study, all reproductive stages had a slightly higher mean instantaneous speed in presence of predators, than those reported by Michalec *et al.* (2010) in absence of predators. These differences may be explained by a higher proportion of fast prey escape responses when exposed to predators. In fact, copepods are known to perform escape responses when perceiving hydromechanical stimuli (Hwang *et al.*, 1994; Hwang and Strickler, 2001). Michalec *et al.* (2010) showed that, in the absence of predators, ovigerous females of *E. affinis* exhibited higher mean instantaneous speeds than both males and females. Our results confirmed this trend with ovigerous females swimming faster than males, which in turn swam faster than females. As highlighted by Tiselius and Jonsson (1990) increased speed generates a stronger hydromechanical signal which, according to Kiørboe and Visser (1999), can be perceived from longer distances. In addition, a fast moving prey is exposed to higher encounter rates with predators (Gerritsen and Strikler, 1977). It is therefore reasonable to attribute the higher vulnerability of ovigerous females to their stronger hydromechanical disturbance and their higher encounter rates with predators. The last hypothesis can therefore be maintained.

In a general predator-prey encounter framework, the ovigerous females which are bigger and swim faster produce stronger hydromechanical disturbance and are more likely to be encountered by larval fish than slower prey. They consequently suffer higher mortality than males and females. Conversely, the females which swim slower than males produce a moderate hydromechanical disturbance and have lower contact rates with predators; which compensates for their bigger size. Accordingly, no mortality differences could be observed between males and females. From a mechanistic perspective, our study implies 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 addition, and as highlighted by Kiørboe and Visser (1999), 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 the prey conspicuousness to predators when modeling the predator-prey encounters in the plankton.

Ecological implications of differential vulnerability of different reproductive stages of *E. affinis*

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 (1996) who observed frequent viable egg detachment in the copepod *Eudiaptomus 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* (Flinkman *et al.*, 1994; Conway *et al.*, 1994) can conserve their viability following ingestion and passage through the gut of planktivorous fishes. Both Redden and Daborn (1991) and 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. However, high nauplii densities were only observed in the low salinity zone (from 0 to 5) (Devreker *et al.*, 2008), which is consistent with their optimal salinity for faster development (Devereker *et al.*, 2004). Devreker *et al.* (2008) attributed this distribution discrepancy to differential swimming behavior across the developmental stages. The rationale is that, contrary to nauplii that are aggregated as passive particles, adults are able of tidal-governed vertical migrations (Morgan *et al.*, 1997) and can spread over wider areas (Devreker *et al.*, 2008). Appealingly, 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* larvae, that 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 ichtyoplankton.

Chapter 6. Negative effects of turbulence on the feeding dynamics in European sea bass (*Dicentrarchus labrax*) larvae on *Artemia* sp. nauplii

6.1 Introduction

Since the pioneer work of Rothschild and Osborn (1988) stating that turbulence enhances the contact rates between plankters, several papers investigated the effect of turbulence on the predator-prey interactions. Subsequent theoretical investigations (MacKenzie *et al.*, 1994; Mariani *et al.*, 2007; Pécseli *et al.*, 2010) and empirical results (MacKenzie and Kiørboe, 1995; Utne-Palm and Stiansen, 2002; Kato *et al.*, 2008) indicated that intermediate turbulence was beneficial to planktivorous predators. In fact, there is a general agreement about a dome-shaped relationship between turbulence and ingestion rates (*e.g.* MacKenzie *et al.*, 1994). The rationale is that ingestions increase, through the enhancement of contact rates and then decrease when the decline of pursuit success outweighs the benefits of increased encounters (Mackenzie *et al.*, 1994). This theory has got support from some field investigations revealing higher growth rates and survival of fish larvae exposed to wind stress areas (Sundby and Fossum, 1990; Muelbert *et al.*, 1994), while as other studies revealed opposite results (*e.g.* Reiss *et al.*, 2002). The dome-shaped relationship hypothesis relies on many assumptions commented in Browman and Skiftesvik (1996) and Browman (1996). One additional assumption is that prey densities should be below the saturating level (Saiz *et al.*, 1992). The validity of this assumption for *in situ* conditions was contested because average field densities are inconsistent with larval search volumes (Pepin, 2004). In fact, at scales relevant to fish larvae, prey distribution is not homogeneous (Young *et al.*, 2009) and consistently reported to be very high (Devreker *et al.*, 2008). In addition, while as turbulence occurs at variable time scales, previous researches mostly focused on a single exposure time, implicitly assuming that feeding dynamics are linear. The present study investigated the effect of a wide range of turbulence levels on the ingestion rates in the European sea bass, *Dicentrarchus labrax* (Linnaeus, 1758), larvae exposed to a realistic prey density as well as their feeding dynamics. Our aims were (i) to examine the effects of turbulent flow on the ingestion rates in sea bass larvae when exposed to a realistically high prey density and (ii) to investigate whether maximum feeding levels are influenced by turbulence.

6.2 Material and methods

6.2.1 Experimental device and turbulence generation

The experiments were conducted at the Laboratory of Oceanology and Geosciences (LOG), Wimereux, France. The experimental device consisted of an oval (2 m large, 1.02 m wide) unidirectional flume (0.3 m height and width) of 300 L (Fig. 14). The lateral walls of the flume were made of transparent acrylic, where as the bottom wall was made of dark grey PVC. The device was filled with 250 L of water. The water salinity was adjusted to 15 by mixing filtered (0.2 μm) seawater and de-ionized water. Flow was generated by the rotation of a set of 10 parallel discs (0.6 m of diameter, Fig. 14). Discs were driven by an electrical engine where rotation frequency was controlled down to the unit level using an electronic control board.

The whole system was lit by 4 light tubes (36 W, Osram lumix plus eco), placed 1 m above the flume, providing a mean light intensity of 15.2 ± 1.1 μmol s^{-1} m^{-2} at the water surface. Experimental room and water temperature were maintained at 18°C.

6.2.2 Velocity measurement

Flow velocity was measured using a Miniature EM current meter (AEM-HR, ALEC electronics) placed at an equal distance from the bottom and the surface of the water at the diametrically opposed side of the rotating discs. The sampling frequency chosen for the current meter was of 2 Hz and the sampling duration was of 2000 seconds.

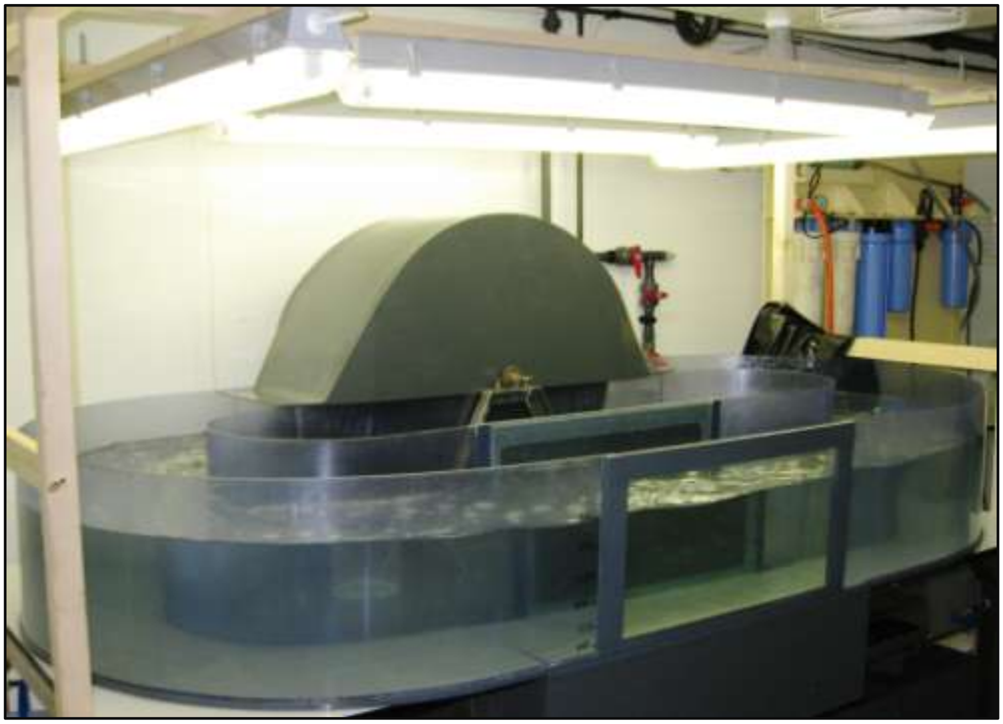

Fig. 14. Photo of the experimental flume used for turbulence generation.

6.2.3 Turbulence estimation

We quantified experimental flow using the mean velocity (*U*) and the Reynolds number (*Re*), using the formula 1 (chapter 2).

6.2.4 Experimental animals

6.2.4.1 Predator

The European sea bass, *Dicentrarchus labrax* (Linnaeus, 1758), is a commercially important euryhaline fish species from western European waters that relies on estuaries as nursery grounds (Kelly, 1988; Cabral and Costa, 2001). In the Seine estuary (English Channel, France), larval stages of this species were regularly collected during our multi-disciplinary sampling programs ZOOTRANZ 2008 and 2009. For the present study, larvae (48 days old, 13.1 ± 1.8 mm) of this species were brought to the Marine Station of Wimereux (France) from a commercial fish hatchery (Ecloserie Marine de Gravelines, France) in May 2009. At the laboratory, fish were separated into 16 groups exclusively fed on freshly hatched *Artemia* sp. nauplii and were kept in a 16:8 (light:dark) cycle at a temperature range of 18-20 °C.

6.2.4.2 Prey

The use of a copepod, which behavior is strongly affected by turbulence (Hwang, 1991), as prey could result in confounding effects. In an attempt to approach the problem from the sole perspective of the predator, we selected *Artemia* sp. a non-evasive plankter as prey (Trager *et al.*, 1994). Freshly hatched nauplii were obtained after incubating *Artemia* sp. cysts during 20-24 h at 24 °C and a salinity of 15.

6.2.5 Experimental procedure

6.2.5.1 Predator density

Groups of 45-50 larvae were used for experiments with feeding duration of 15 min, and groups of 10-15 fish were used for experiments with longer feeding duration. All fish were devoid of any food for 24 hours preceding the experiment. This starvation duration was chosen on the basis of our own previous experiments on gut clearance time, which indicated that 24 hours were sufficient to ensure total gut clearance. Due to the high number of treatments, fish were tested at different hours of the day. Accordingly, the photoperiod was delayed for the corresponding groups so that fish were always tested 2 hours after the onset of the light period.

6.2.5.2 Prey density

Since *Artemia* sp. is not naturally present in the habitat of sea bass larvae, we had to use a density consistent with densities of prey similar in size, that prevail in that environment. In the Seine estuary, one of the main zooplankton species is *E. affinis* (Devreker, 2007). Copepodids I to IV of this species fall into the size range of freshly hatched *Artemia*. We consequently used densities of 200 ind. L^{-1} of *Artemia* sp., comparable with the densities of CI-CIV of *E. affinis* reported from fine-scale sampling in the Seine estuary (Devreker, 2007). Pilot experimentations revealed that this density was not saturating to sea bass of comparable size.

6.2.5.3 Experiment 1: Effect of turbulence on the ingestion rates in sea bass larvae

Ingestion rates in sea bass larvae were tested for one calm and 15 turbulent treatments (Table 8). Prior to each treatment, a group of 45-50 larvae was allowed to acclimatize to the experimental room temperature and light during 15 min. Then, prey were added into the flume, and the motor driving the discs was turned on at a 2 Hz (0.08 m s^{-1}, *Re* = 18100) for 5 min to even out *Artemia* sp. distribution. Afterwards, the desired rotation frequency (Table 8) was set on and flow was allowed to stabilize for 10 min. Thereafter, fish were gently introduced into the flume; a 2 L beaker containing the fish was slowly immersed in water, with its bottom facing the flow, at an angle of about 60° with the water surface, allowing larvae to freely swim into the channel. This operation never lasted more than 30 s. After 15 min, fish were removed from water and preserved in ethanol. All of the fish were consequently measured, their guts dissected and the contents enumerated under a dissecting microscope. During dissections, special care was taken to verify whether prey items were present in the intestines which may reveal possible food defecation. After each treatment, the whole water volume was filtered on a 50 µm mesh in order to remove all prey, and the procedure was repeated as described above.

Table. 8. Motor rotation frequencies and corresponding current velocity (*U*) and Reynolds number (*Re*). The dissipation rates produced by our experimental device ranged from 3.53×10^{-5} m^2 s^{-3} for a rotation frequency of 1 Hz to 1 m^2 s^{-3} for a rotation frequency of 15Hz. For comparison, maximum mean current velocities registered in the Seine estuary (natural habitat of *Dicentrarchus labrax* larvae) range from 0.8 m s^{-1} at the surface to 1.8 m s^{-1} at the bottom (Devreker *et al.*, 2008). A rough estimation of *Re* for a mean temperature of 15 °C, a water depth range of 4.5-11 m and a salinity range of 0-25, gives a maximum *Re* range of 1.13×10^6-2.21×10^6.

Frequency (Hz)	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
U (m s^{-1})	0	0.04	0.08	0.12	0.17	0.20	0.25	0.29	0.33	0.38	0.42	0.47	0.51	0.55	0.60	0.64
Re (x10^3)	0	8.70	18.10	28.00	37.90	47.80	57.70	67.60	75.70	87.40	97.30	107.10	117.20	127.10	136.90	146.80

6.2.5.4 Experiment 2: Combined effect of turbulence and exposure duration on ingestion rates in sea bass larvae

For this experiment, one calm and two turbulent levels corresponding to mean flow speeds of 0, 0.25 and 0.51 m s^{-1} (*Re* = 0, 57700 and 117200, respectively) were used. For each treatment, 7 time increments: 2.5, 5, 10, 15, 30, 60 and 90 min were tested. A total of 512 fish (42 groups of 10 to 15 larvae) were used for this experiment. The whole experimental procedure is similar to the one described for experiment 1. However, two replicates were performed for each treatment (*i.e.* 2 × turbulent level × exposure time).

6.3 Results

6.3.1 Predator behavior

In the calm treatment, fish larvae colonized the entire flume. In the turbulence treatments, fish preferred to shelter close to the lateral and bottom walls of the flume. When exposed to stronger current in other parts of the flume, fish actively swam to maintain their position against the flow. Starting from U = 0.42 m s^{-1} (Re = 97300), fish did not continuously swim against the flow; rather, they performed short swimming bursts to relocate themselves in the water column. Starting from U = 0.55 m s^{-1} (Re = 127100), relocating bursts could not be observed and larvae were constantly advected by the flow.

No fish mortality was recorded after the turbulence exposures. Similarly, no signs of external injuries were detected on fish during larval dissections.

6.3.2 Experiment 1: Effect of turbulence on the ingestion rates in sea bass

The mean prey ingestion rates in the sea bass larvae were lower in turbulent conditions than in calm condition. Across the 15 experimental levels of turbulence, the increasing *Re* resulted in decreasing rates of ingestion (Fig. 15 A and B). Starting from Re = 127100 (U = 0.55 m s^{-1}), larvae were unable to feed. The increasing flow level enhanced the coefficient of variation (CV, Fig. 16). Nevertheless, CV values were almost constant (CV = 44-45%) for the first 5 flow levels.

Mean ingestion rates decreased exponentially (Figs 15 A and 19 A; R^2 = 0.91) while as CV of ingestions increased exponentially (Fig 16 A; R^2 = 0.82).

6.3.3 Experiment 2: Combined effect of turbulence and exposure duration on the ingestion rates in sea bass larvae

For all exposure durations, no *Artemia* sp. individuals were observed in the intestine of fish proving that larvae did not defecate during experiments. Regardless of feeding duration (2.5~90 min), turbulence levels (Re = 57700 and 117200) diminished ingestion rates, with the highest flow level (Re = 117200) being associated with the most pronounced downsides (Fig. 17 A and B). Ingestion response to time exposure followed a logarithmic trend (R^2 = 0.94, 0.85 and 0.91 for Re = 0, 57700 and 117200, respectively). The larvae were not able to reach to the satiation

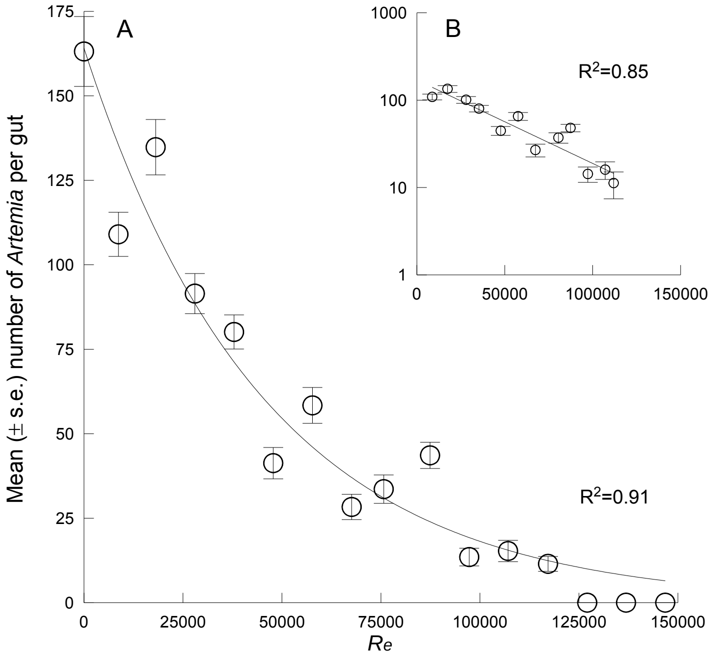

Fig. 15. Ingestion rates of *Artemia* sp. by *Dicentrarchus labrax* larvae (mean ± s.e.) as a function of Reynolds number (*Re*). Linear-linear plot (A), linear-log plot without the null values (B). The solid lines represent the exponential fit; $Y = e^{-0.00002X} \times 164.07$ (A) and $Y = e^{-0.0002X} \times 169.78$ (B) (n = 766).

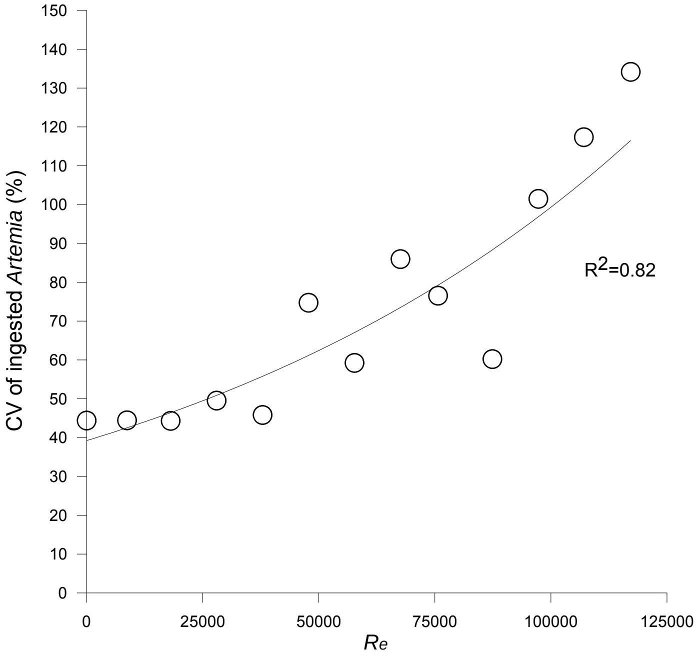

Fig. 16. Inter-individual variability expressed as the coefficient of variation (CV, %) in mean ingestions of *Artemia* sp. by *Dicentrarchus labrax* larvae as a function of Reynolds number (*Re*). The solid line represent the exponential fit; $Y = e^{0.000009X} \times 0.39$ (n = 766).

level in 15 min of exposure duration, supporting the choice of this exposure duration for the experiment 1. The prey ingestion rates were close to the asymptotic limit for all flow treatments after 90 min of exposure duration. Turbulence negatively affected the maximum intake levels as minimum values were observed for the highest turbulent treatment.

6.4 Discussion

6.4.1 Flow properties

Energy dissipation rate (ε) has been often used in experimental studies investigating the effects of turbulence on the predator-prey interaction (*e.g.* Utne-Palm and Stiansen, 2002; Oshima *et al.*, 2009). The energy dissipation is an important quantity to characterize turbulence at smallest scales, but is should also be complemented by the Reynolds number information; both are useful to characterize the nature of the turbulent flow. Moreover, recent numerical simulations, demonstrated that plankton encounter rate is Reynolds number-dependent (Humphries, 2009). In estuaries, maximum Reynolds numbers typically range from 1×10^5 to 1×10^8 (Trevethan *et al.*, 2007) whereas dissipation rates are on the order of 10^{-3} m^2 s^{-3} (MacDonald, 2003). In our experiments, we tested the ingestion rates in sea bass larvae in one calm and 15 turbulent treatments with *Re* ranging from 8.7×10^3 to 1.4×10^5 and energy dissipations ranging from 3.53×10^{-5} m^2 s^{-3} to 1 Hz to 1 m^2 s^{-3} consistent with flow properties reported from the field. In this study all tested flows, excepting the calm water treatment, were turbulent. It is worth noticing that energy dissipation rates reported here may be higher than what would have been observed for a similar flow in open ocean conditions. In fact, dissipation rates are higher at the proximity of solid walls (Teixeira and Belcher, 2000). Therefore, unless using very large experimental devices in order to avoid the wall effects, energy dissipation rates (ε) may be misleading when comparing experimental estimations to *in situ* conditions.

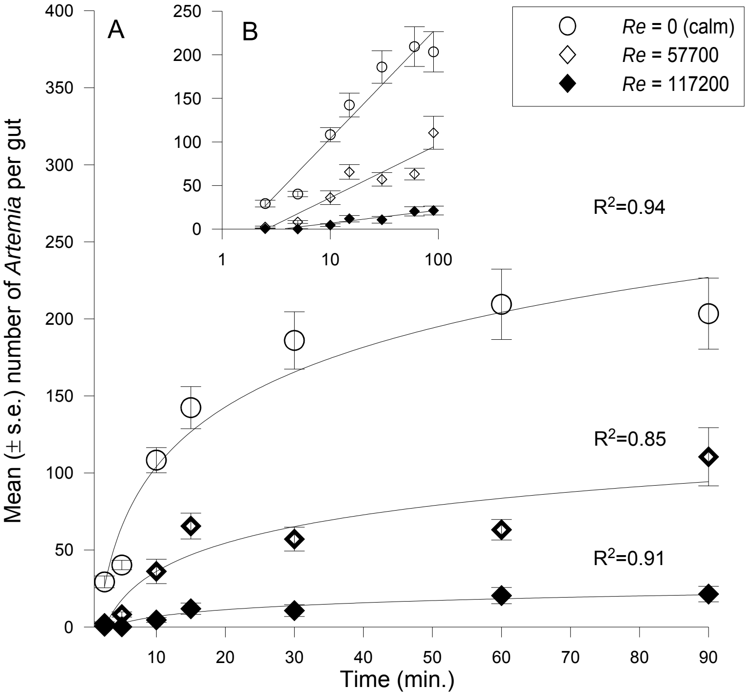

Fig. 17. Ingestion rates of *Artemia* sp. by *Dicentrarchus labrax* larvae (mean ± s.e.) as a function of time across three turbulence levels. Linear-linear plot (A), log-linear plot (B). Solid lines represent the logarithmic fit; $Y = 55.93 \times \ln(X) - 24.77$ (A, 0Hz); $Y = 26.51 \times \ln(X) - 25$ (A, 6Hz); $Y = 6.44 \times \ln(X) - 8.02$ (A, 12Hz) ($n = 512$).

6.4.2 Effect of turbulence on the ingestion rates in sea bass

Our results suggested that turbulence exerted negative effects on ingestion rates in larval fish feeding on non-evasive prey at a density commonly recorded in the natural environment of sea bass larvae (*i.e.* 200 ind. L^{-1}). These observations are contradictory with two empirical investigations reporting beneficial effects of moderate turbulence on the ingestions rates in larval Pacific bluefin tuna, *Thunnus orientalis*, (Kato *et al.*, 2008) and Japanese flounder, *Paralichthys olivaceus*, (Oshima *et al.*, 2009) on rotifers (non-evasive prey). We explain these discrepancies by differences in the methodology. In fact, both Kato *et al.* (2008) and Oshima *et al.* (2009) used water bubbling in their control treatment (*i.e.* calm treatment) which prevents us from confronting the ingestions observed in turbulent flow to ingestions observed in a calm water condition. In order to overcome such difficulty, we used calm water ($U = 0$; $Re = 0$) as a control in our experiments.

Ingestion rates integrate the whole sequence of events occurring during the predator-prey interaction. However, turbulence may affect all of: the encounter, the pursuit, the attack (MacKenzie and Kiørboe, 1995) and the capture (MacKenzie and Kiørboe, 2000) events separately. Hereafter, we attempt to combine the results of the observed ingestions within a framework of turbulence effects on the whole predator-prey interaction.

Turbulence increases contact rates between planktonic organisms (Rothschild and Osborn, 1988) which renders moderate turbulence levels beneficial at prey densities below saturation (Mackenzie *et al.*, 1994; Saiz *et al.*, 2003). Hydromechanical detection of prey is largely documented in fish (*e.g.* Montgomery *et al.*, 2000), including sea bass larvae (see chapter 5). On the downside, turbulence may blur hydromechanical signals and affect the sensory field of plankters (Yen *et al.*, 2008). In addition, turbulence is detrimental for pursuit success, which has been demonstrated both theoretically (Kiørboe and Saiz, 1995; Kiørboe and Mackenzie, 1995; Mariani *et al.*, 2007) and empirically (Mackenzie and Kiørboe, 2000). The underlying mechanism is that prey may be advected out of the perceptive area of the fish faster than the reaction of the fish, leading to unsuccessful pursuits (Mackenzie and Kiørboe, 2000). Our results showed an exponential decrease of feeding across turbulence and corroborated the theoretical results of Mariani *et al.* (2007) who predicted an exponential decay of pursuit success of larval fish with turbulence. Finally, turbulence is assumed to be of no effect on the attack success because an attack is operated quickly (MacKenzie and Kiørboe, 2000) and at very short distances from the prey (MacKenzie *et al.*, 1994). This has been experimentally verified for cod larvae

(MacKenzie and Kiørboe, 2000). We may accordingly neglect the effects of turbulence on the attack success of larval sea bass. In summary, larval feeding under turbulence is affected by i) increased encounter rates, ii) decreased perception ability and iii) decreased pursuit abilities (see chapter 2). The above mentioned factors will not only affect the mean ingestion rates, but also the inter-individual variability in ingestion rates. Benefits of more encounters were not high enough to sustain high feeding in sea bass larvae across turbulence. However, they balanced the drawbacks of lower perception and pursuit abilities on the inter-individual variability for velocities ranging from $U = 0.04$ m s^{-1} ($Re = 8700$) to $U = 0.17$ m s^{-1} ($Re = 37900$). In fact, for that turbulence range, the CV of ingestion rates was relatively constant (CV = 44-45%) and equal to the CV observed for the calm treatment, in which feeding was only affected by intrinsic inter-individual variability. At higher *Re*, feeding decreased and inter-individual variability increased with turbulence, indicating that the decrease of pursuit abilities and pursuit success outweighed the benefits of more encounters, most likely because the encounter rate reached its saturating threshold.

6.4.2.1 Relevance to the natural environment

In the natural environment of sea bass larvae (*i.e.* Seine estuary), Devreker *et al.* (2008) reported mean flow velocities ranging from 0.25 m s^{-1} to nearly 2 m s^{-1} ($Re = 1.13\times10^6$-2.21×10^6) except during the tidal current reversal. Our experiments showed that the steepest decline of feeding occurred from the onset of turbulence ($U = 0.03$ m s^{-1}; $Re = 8700$) to average flow velocities of 0.3 m s^{-1}. In addition, at mean velocities higher than 0.55 m s^{-1} ($Re = 127100$), larval feeding was totally impeded. In spite of all of the above mentioned limitations, *in situ* studies revealed the dependency of larval and juvenile of European sea bass on estuaries of the English Channel (Kelly, 1988; Laffaille *et al*., 2001b) including the Seine estuary (Dauvin and Desroy, 2005) for their growth and recruitment. We hereafter suggest some explanations to this inconsistency. First, larvae can avoid *in situ* detrimental flow velocities through migration towards less turbulent areas as reported for larval capelin (*Mallotus villosus*) and Atlantic herring (*Clupea harengus*) in the Saint Laurence estuary (Fortier and Legget, 1983). Second, sea bass of the Seine estuary might exhibit an intermittent feeding strategy during the short current reversal periods between flood and ebb as reported by Laffaille *et al.* (2001) for 0-group sea bass of the Mont Saint Michel Bay (France, English Channel). In fact, young of the year of sea bass are able to consume large quantities (8% of their body weight) of food during the short period (1-2 h) of tidal submersion in the Mont Saint Michel Bay (Laffaille *et al*., 2001). Finally, even though mean flow velocities recorded in the Seine estuary seemed detrimental to mean ingestions rates, large inter-individual differences ($60\ \% < CV < 134\ \%$) observed at velocities higher than $0.17\ m\ s^{-1}$ ($Re > 37900$) suggest that a substantial proportion of fish larvae were still able to feed at high flow intensities. This indicates that detrimental effects of turbulence might be overestimated through the sole investigation of mean ingestion values.

6.4.3 Combined effect of turbulence and exposure duration on the ingestion rates in sea bass

Ronzani Cerqueira (1986) revealed that the required time for sea bass larvae (mean TL = 12.4 ± 0.67 mm) to start evacuating food while feeding on *Artemia* sp., ranged from 150 to 210 min as prey densities decreased from 15000 L^{-1} to 1000 L^{-1}. This is consistent with our observations that sea bass larvae used in this experiment (mean TL = 13.1 ± 1.8 mm) did not defecate food after 90 min of feeding at a prey density of 200 L^{-1}.

The cruise swimming speed (speed which can be sustained for an extended period of time) of fishes, as well as their swimming performance, are inversely proportional to turbulence (Pavlov *et al.*, 2000). It is also known that energy expenditure of fishes increases with increasing turbulence (Pavlov *et al.*, 2000; Enders *et al.*, 2003) and that individuals that reach their energetic limit are unable to overcome the flow (Pavlov *et al.*, 2000). This can be elicited in the light of prey profitability. In fact, at higher levels of turbulence, a larval fish has to spend more energy in swimming and stabilizing itself against the flow while searching and pursuing prey. This may renders a prey less profitable in turbulent conditions. Our results demonstrating that larval fish maximum feeding levels decrease as turbulence increases are consistent with a differential energy expenditure across turbulence levels. We accordingly pinpoint that maximum feeding levels observed in ideal (calm water) laboratory conditions, may not be directly extrapolated to turbulent conditions.

We remind here that we used *Artemia* sp., a non-evasive prey, as a model. Using a prey that may only represent the non-evasive fraction of the plankton (Trager *et al.*, 1994) makes our results only representative of the effect of turbulence on predator-prey interaction from the sole perspective of the fish larva. In fact, naturally occurring prey of sea bass larvae, *i.e.* copepods (Pauly and Christensen, 1995), may be much more motile. For example, copepods are known to display escape responses as fast as 0.5 m s^{-1} (Buskey *et al.*, 2002). However, in a turbulent environment, the perceptive abilities of copepods can be affected (Jiménez, 1997; Kiørboe, 2008; Yen *et al.*, 2008), which would favor higher ingestion for fish larvae. In order to address that issue, we report in the following chapter the results of an investigation of the effects of turbulence on the feeding of sea bass juveniles on the copepod *Eurytemora affinis*.

Chapter 7. The effects of turbulence on the feeding in sea bass juveniles on live versus dead *Eurytemora affinis* (Copepoda, Calanoida)

7.1 Introduction

In western Europe, larvae and juveniles of the euryhaline fish sea bass (*Dicentrarchus labrax* L.) colonize estuaries, which represent their nursery areas, during spring (Kelly, 1988; Cabral and Costa, 2001; Laffaille *et al*., 2001). In the Seine estuary (English Channel, France), one of the most abundant copepods *Eurytemora affinis* (Mouny and Dauvin, 2002; Devreker, 2007; Devreker *et al.*, 2008), is mainly preyed upon by larvae and juveniles of *D. labrax* (Mouny *et al.*, 1998). Early stages of *D. labrax* are pause-travel predators which detect their prey during pause events occurring between swimming bouts dedicated to relocation (Georgalas *et al.*, 2007). This strategy is intended to facilitate the discrimination of moving prey from inert material in species living in areas with high densities of suspended matter, *i.e.* estuaries and coastal areas (Janssen, 1992). In such areas, dead individuals can represent up to 40% of the copepod population and are a consistent feature of the zooplankton (Tang *et al*., 2006; Elliot, 2010). In the Seine estuary, turbulence can influence the feeding of *D. labrax* not only through the resuspension of dead copepod carcasses into the water column but also as a result of contact rates enhancement (Rothschild and Osborn, 1988). Accordingly, two questions can be raised about the *D. labrax-E. affinis* interaction in the Seine estuary:

i) If *D. labrax* individuals rely on movement to discriminate living prey from non-edible material, can they distinguish copepods' own motion from turbulence-driven motion?

ii) How does turbulence affect the feeding rates of *D. labrax* juveniles on realistic densities of copepods?

In order to elucidate these questions, we investigated the effect of turbulence on the feeding rates in *D. labrax* juveniles on both live and dead *E. affinis* offered at a realistic density.

7.2 Material and methods

7.2.1 Experimental setup

In order to maintain a relatively constant prey density during the whole experiment duration, we used a relatively large experimental volume in comparison to experimental volumes previously used in similar studies (Table 9). For this study, we used the experimental device described in chapter 6 (Fig. 14). The experimental conditions were similar to those described in chapter 6. Briefly, the flume was filled by water (salinity: 15) until reaching a height of 25 cm corresponding to a total volume of 250 L. A mean illumination of 15.2 ± 1.1 µmol s^{-1} m^{-2} was provided by 4 light tubes (36 W, Osram lumix plus eco) placed 1 m above the flume. Room and water temperature were maintained at 18 °C. Flow velocity was measured using a current meter (AEM-HR, ALEC electronics). Flow was quantified using the Reynolds number (*Re*).

7.2.2 Experimental animals

We used 60 days old (21.9 ± 3.1 mm total length) sea bass juveniles originating from a commercial hatchery (Ecloserie Marine de Gravelines, France). At the laboratory, fish were progressively (over 12 h) adapted from their rearing salinity of 32 to the experimental salinity of 15. Animals were thereafter maintained in a 16:8 (light:dark) light regime at a temperature of 18-20 °C and fed daily on the copepod *E. affinis*. 24 h before each experiment, one group of 40-45 fish was devoid of food in order to ensure complete gut clearance.

Eurytemora affinis were collected from the Seine estuary by means of WP2 oblique tows during ebb tide near the Tancarville Bridge where maximum abundances of this species occur

Table. 9. Review of studies investigating the effect of water flow on the fish-copepod interaction with emphasis on prey densities, experimental volumes and flow velocities. For Utne-Palm and Stiansen (2002) and Utne-Palm (2004) only dissipation rates are provided.

Author	**Parameter**	**Predator**	**Prey**	**Prey density**	**Volume**	**Flow characteristics**
Chesney, 1989	Growth and survival	*Morone saxatilis* (1 to 20 days old)	*Eurytemora affinis* 70% nauplii 30% copepodites and adults	50 ind. L^{-1} 100 ind. L^{-1} 250 ind. L^{-1}	32 L	0 and 0.06 m s^{-1}
MacKenzie and Kiørboe, 1995	Attack rates	*Gadus morhua* (5.2 mm and 6.1 mm) *Clupea harengus* (8.7 mm)	*Acartia tonsa* nauplii	4 ind. L^{-1} 1500 ind. L^{-1}	52 L	0 to 4.5×10^{-2} m s^{-1}
MacKenzie and Kiørboe, 2000	Pursuit success	*Gadus morhua* (8.7 mm and 12.3 mm)	*Acartia tonsa nauplii* and early copepodites	100 ind. L^{-1}	17.7 L	0 to 1.2×10^{-2} m s^{-1}
Utne-Palm and Stiansen, 2002	Attack rates and swimming activity	*Clupea harengus* (15, 20, 23, 26 and 28 mm)	*Acartia tonsa* nauplii	20-30 ind. L^{-1}	62 L	0 to 5.4×10^{-5} m^{2} s^{-3}
Utne-Palm, 2004	Attack rates and swimming activity	*Clupea harengus* (20, 23 and 29 mm)	*Acartia tonsa* nauplii	20 ind. L^{-1}	62 L	0 to 8×10^{-6} m^{2} s^{-3}
Clarke *et al.*, 2005	Foraging behavior and capture success	*Acanthemblemaria* *Spinosa* and *A. aspera* (21-25 mm)	*Acartia tonsa* adults	Not mentioned	0.5 L	0 to 0.2 m s^{-1}
Clarke *et al.*, 2009	Foraging effort and capture success	*Acanthemblemaria spinosa* and *A. aspera* (21-25 mm)	*Acartia tonsa* adults	16-33 ind. L^{-1} 5-6 ind. L^{-1}	3 L 17 L	0.03 to 0.4 m s^{-1}

(Devereker *et al.*, 2008). This sampling allowed the collection of the large quantities of monospecific copepods necessary for the experiment. Animals were transported to the Marine Station of Wimereux (Laboratory of Oceanology and Geosciences, Wimereux, France) and kept in 40 L tanks at a salinity of 15, a temperature of 18-20 °C, and a photoperiod of 16:8 (light:dark). Copepods were fed daily on the red algae *Rhodomonas marina*. For predation experiments, only *E. affinis* adults retained by a 400 μm sieve were used. This ensured a prey to predator size ratio range of 0.03-0.05.

7.2.3 Experimental procedure

Feeding rates in *D. labrax* juveniles across turbulence were investigated using either live or dead copepods as prey separately. When live copepods were used, ingestion rates were tested for one calm and 5 turbulent levels. When dead copepods were used as prey, only 5 turbulent levels were tested. In fact, using dead prey in a calm treatment would have resulted in the sinking of all copepods to the bottom of the flume. Copepods were frozen-killed (-15 °C during 1 h) in order to conserve their color integrity. The experimental flow velocities (*U*) and corresponding *Re* are summarized in table 10.

Table. 10. Motor rotation frequency, Mean current velocity (*U*) and corresponding *Re* conditions tested for each of the prey types (L: live copepods, D: dead copepods).

Rotation Frequency (Hz)	0	2	4	6	8	10
U **(m s^{-1})**	0	0.08	0.17	0.25	0.33	0.42
Re	0	18100	37900	57700	75700	97300
prey	L	L and D	L and D	L and D	L and D	L and D

Prior to each test, a nominal number of copepods was added into the flume as to reach a density of 100 ind. L^{-1} consistent with maximum densities of adult *E. affinis* reported from the Seine estuary (Devreker *et al.*, 2008). In order to homogenize prey distribution, the motor was run during 5 min at a rotation frequency of 2 Hz. Afterwards, the desired experimental rotation frequency was set, and the flow allowed to stabilize during 10 min. One group of ~40 fish, previously acclimatized to room temperature and light conditions for 15 min, was gently introduced into the channel and allowed to feed for 15 min. Finally, fish were removed from the experimental channel and preserved in ethanol for subsequent gut content enumeration and size measurements.

7.2.4 Data analysis

For each prey type mean ingestions across turbulence were compared using the non-parametric Kruskal-Wallis test (K-W). Then, means were compared pair-wise using a Wilcoxon test and a Bonferroni correction to determine which means are different from each others. For each flow level, mean ingestions of live versus mean ingestions of dead prey were compared using the Wilcoxon test.

The ratio of live to dead $R_{L/D}$ ingested copepods for each flow level was computed as follows:

$$R_{L/D} = \frac{L_t}{D_t} \tag{12}$$

with L_t the mean number of live copepods ingested at a turbulence level t and D_t the mean number of dead copepods ingested prey at the same turbulence level t.

7.3 Results

Ingestion rates were always higher when fish were offered live copepods (Fig. 18). When live copepods were used as prey, the ingestion rates followed a dome-shaped relationship with turbulence, reaching a maximum value of 102.5 copepod × fish^{-1}. When dead copepods were used, increasing turbulence resulted in decreasing ingestion rates. For both prey types, the optimal flow level for fish ingestions was Re = 18000 (Fig. 18).

The differences in ingestions between live and dead copepods decreased as turbulence increased (Fig. 18 and Table 11).

The inter-individual variability in ingestions of live copepods followed a sigmoid trend with comparable CV values (35%) for the calm and the first turbulent treatment (*Re* = 18100) (Fig. 19).

Table. 11. P values of the Wilcoxon test for mean number of ingested live copepods versus dead copepods as function of *Re*.

Re	**18100**	**37900**	**57700**	**75700**	**97300**
Mean (± s.e.) live copepods per fish	102.47±4.87	51.90±3.24	22.18±3.76	0.62±0.27	1.60±0.81
Mean (± s.e.) dead copepods per fish	28.60±2.63	0.66±0.22	0	0.12±0.05	0.78±0.32
P value	0.00	0.00	0.00	0.39	0.60

The ratio of live to dead ingested copepods ($R_{L/D}$) exhibited a dome-shaped relationship across turbulence with ratios ranging from 2 to 77 times (Fig. 20).

7.4 Discussion

7.4.1 Data analysis

A statistical experimental unit is the smallest system to which a single treatment is applied and which is dealt with independently of other such systems (Cox, 1958 *in* Kovlov and Hurlbert, 2006). In 1984, Hurlbert defined *pseudoreplication* as the exploitation of *evaluation units* from a single *experimental unit* as independent replicates (Hurlbert, 1984). He advocated that, in such cases, the use of inferential statistics would not be informative, because the *evaluation units* are not statistically independent (Hurlbert, 1984). According to the definition of Hurlbert (1984), our experiment fall into the category of *pseudoreplication* having many *evaluation units* (*i.e.* fish) into the same *experimental unit* (*i.e.* flume), and the use inferential statistical tests might not be accurate in this case. In opposition, Oksanen (2001) argued that such designs are valid, and that inferential statistics should always be used. While reviewing studies of larval fish behavior, we

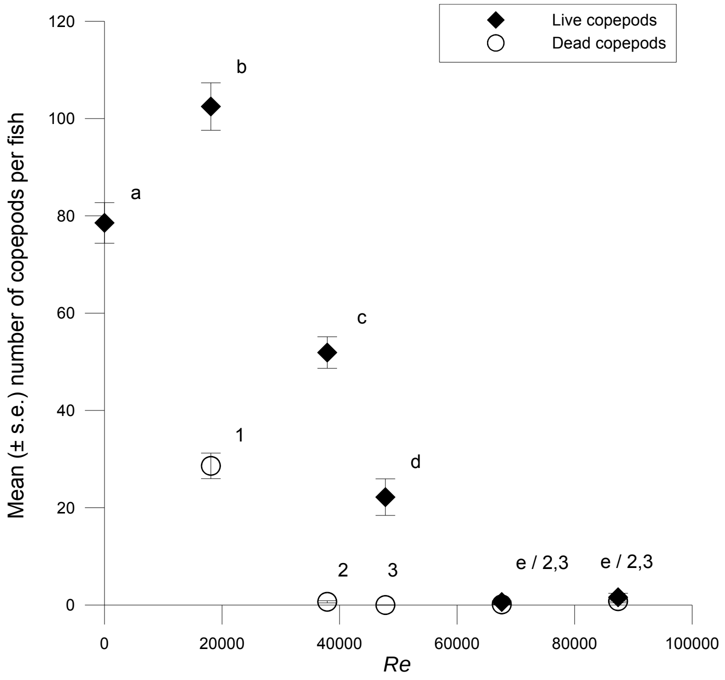

Fig. 18. Mean (± s.e.) number of copepods per gut of *Dicentrarchus labrax* as function of the *Re* for both prey types. Different letters (for live copepods) and numbers (for dead copepods) indicate statistically significant means at $\alpha = 0.05$ (n = 443).

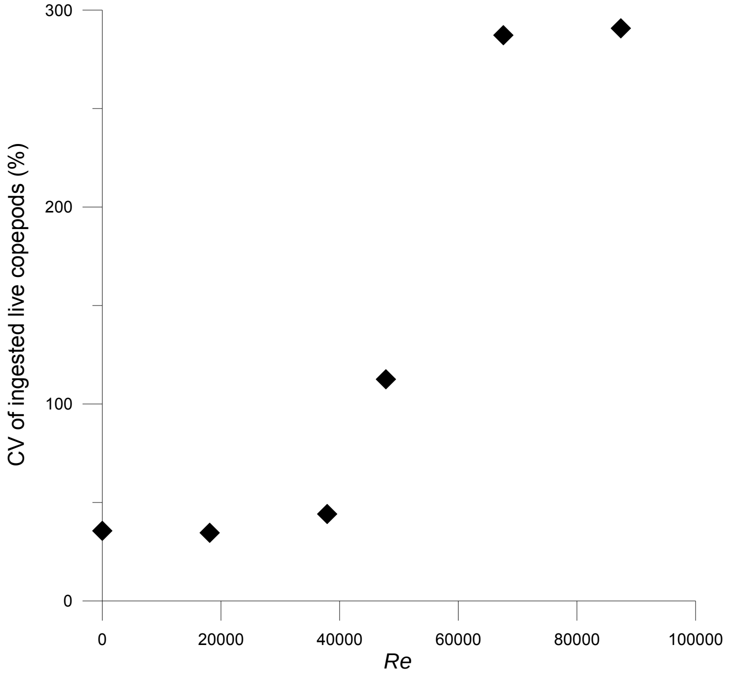

Fig. 19. Inter individual variability expressed as the coefficient of variation (CV, %) in mean ingestions of live *Eurytemora affinis* by *Dicentrarchus labrax* (n = 293).

found that cases falling into Hurlbert's (1984) definition of *pseudoreplication* are common (e.g. MacKenzie and Kiørboe, 1995; Viitasalo *et al*., 1998; MacKenzie and Kiørboe, 2000). Though acknowledging the existence of a debate concerning the validity of inferential statistics tests for experimental setups like ours, we herein gave the results of such tests for the reader's reference.

7.4.2 Feeding of *D. labrax* juveniles on live versus dead copepods

Preference of live prey over dead one is a widespread behavior in fish (Irvine and Northcote, 1983; Nelson and Coull, 1989; Diaz *et al.*, 2003). Indeed, planktivorous estuarine fish rely on plankters' movement to discriminate suitable prey items from inert particles (Janssen, 1992; Buskey *et al.,* 1993). One additional reason for this behavior is that a moving prey has higher probabilities of encountering predators than a motionless one (Gerritsen and Strickler, 1977; Visser and Kiørboe, 2006). In sea bass, the ability to detect movement is favored by the presence of a high density of rods on the retina (Mani-Ponset *et al.,* 1993). The present study did not investigate the selectivity of sea bass juveniles when offered live and dead copepods simultaneously. However, the comparison of ingestion rates observed with live prey versus the ingestions of dead prey revealed that *D. labrax* consistently ingested more live than dead copepods as turbulence increased. This suggests that sea bass juveniles are able to discriminate *E. affinis* intrinsic behavior from motility due to turbulence advection. Due to microbial decomposition, dead zooplankters suffer a loss of organic matter (Elliot, 2010). Accordingly, a reduced feeding activity on dead copepods would avoid sea bass juveniles to waste energy in capturing less profitable prey. Sea bass foraging mechanism seems therefore to be adapted to waters where large amounts of dead copepods and also inert material might interfere with efficient feeding.

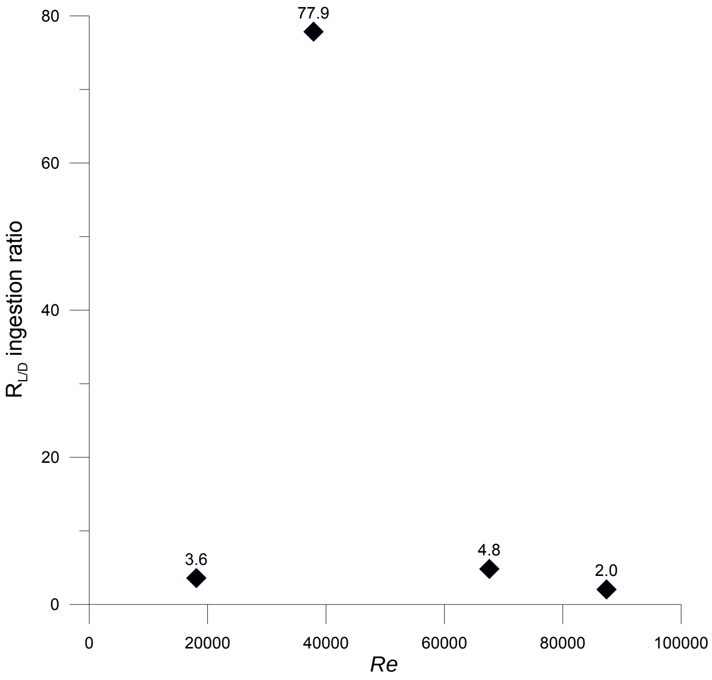

Fig. 20. **Ratio of mean number of live to dead copepods (*$R_{L/D}$*) ingested by *Dicentrarchus labrax* as function of the *Re* (n = 398).**

7.4.3 Feeding of *D. labrax* juveniles across turbulence

For fish, the successful predator-prey interaction sequence comprises the encounter, the pursuit, the attack, the capture and the ingestion. Turbulence is acknowledged to enhance the contact rates of plankters (Rothschild and Osborne, 1988; Mackenzie *et al.*, 1994; Pécseli *et al.*, 2010) and to impede the pursuit success of predators (Mackenzie and Kiørboe, 2000). Using *Artemia* sp. as prey, we demonstrated that turbulence was detrimental to larval sea bass feeding at a realistic prey density (chapter 6 of this study). Conversely, our present results indicated that intermediate turbulence was beneficial to ingestion rates in sea bass juveniles when feeding on live copepods. We attribute this inconsistency to differential escape abilities in *Artemia* sp. and *E. affinis*. In fact, while *Artemia* sp. is a non-evasive plankter (Buskey *et al.*, 1993; Trager *et al.*, 1994), copepods are highly evasive with some species being reported to accelerate faster than 100 m s^{-2} (Buskey *et al.*, 2002; Buskey and Hartline, 2003). In copepods, hydromechanical cues of an approaching predator can trigger an escape response (Hwang and Strickler, 2001; Wagget and Buskey, 2007). Turbulence distorts hydromechanical signals and impedes perception abilities in planktonic prey (Jiménez, 1997; Gilbert and Buskey, 2005; Robinson *et al.*, 2007; Yen *et al.*, 2008), thus increasing the capture success in predators (Clarke *et al.*, 2005). In this investigation, 4 factors were likely to affect feeding: i) increased encounter rates, ii) decreased perception ability in prey, iii) decreased perception ability in predators and iv) decreased pursuit abilities. The observed evolution of ingestion rates across turbulence suggest that the benefits of more encounters and decreased perception abilities of prey outweighed the downsides of limited perception and pursuit abilities in predators for *Re* = 18100. At higher turbulence levels mean ingestions decrease reveals unsteadiness in favor of decreased perception and pursuit abilities of juvenile fish. The evolution of inter-individual variability in ingestions across turbulence supports the above. In fact, at the first turbulent treatment (*Re* = 18100), the CV was equal to what observed in the calm treatment (a proxy of intrinsic variability in absence of turbulence). When prey were dead, feeding could not be tested in calm water and the effects of turbulent versus calm water could not be confronted. However, when comparing the variation of ingestion rates across turbulence, only negative effects could be observed, which is consistent with the negative effects of turbulence for planktivorous fish feeding on non-evasive prey as reported in chapter 6 of this study.

Chapter 8. Conclusions and perspectives

8.1 Fish larvae-prey interactions in calm and turbulent environments

Spatio-temporal co-occurence of fish larvae and their planktonic prey is a requisite for a good recruitment. However, in the natural environment interactions do not occur at the population level, but rather at the individual level (Kiørboe, 2008). Larval fish successful feeding is therefore highly determined by individual predator-prey encounters. At the individual level, encounters are governed by plankter's motion which in turn can be the result of an active swimming behavior or a passive turbulence-advection. In this dissertation, we addressed the flexibility of larval and juvenile fish foraging behavior to changes in the biotic and abiotic environments. We used different biological models from different aquatic habitats. In each application we illustrated the observed results in a general framework. Our main findings were:

1) The swimming behavior of malabar grouper (*Epinephelus malabaricus*) larvae showed differential swimming behaviors in response to prey availability. In fact, in absence of prey, larvae adopted a multifractal anisotropic swimming behavior characterized by large amplitude movements and a higher complexity on the vertical axis. This behavior was consistent with a horizontal distribution of prey patches in the natural environment (Haury and Wiebe, 1982; Gallager *et al.*, 2004). Once predators were exposed to prey, they switched to an isotropic slow swimming behavior in order to remain inside food patches and to maximize encounters with prey. The existence of anisotropy in swimming behaviors of planktonic predators reveals the importance of investigating plankton behavior on the vertical and horizontal projections rather than solely investigating it on the 3D.

2) Shifts in search behavior are regularly explained as being adaptive responses intended to maximize encounters (*e.g.* Coughlin *et al.*, 1992). Nevertheless, the ultimate aim of predator is not to encounter prey, but rather to ingest it. Our study, based on scale-independent metrics, described how swimming complexity during prey pursuit and attack affected the capture success in whitefish (*Coregonus lavaretus*) larvae feeding on wild zooplankton. This focuses attention on the fact that a behavior intended to maximize the encounters may, on the downside, affect the capture success.

3) Ovigerous females (*i.e.* females carrying eggs) of several species of copepods have been reported to be more vulnerable to predation than non-ovigerous females and males. Higher vulnerability of ovigerous females was consistently attributed to their lower escape abilities. In the present investigation, we observed that ovigerous females of the estuarine copepod *Eurytemora affinis* suffered the highest mortality rates when exposed to sea bass larvae. Surprisingly, we also uncovered that ovigerous females of *E. affinis* exhibited the fastest accelerations among all reproductive stages (males, non-ovigerous females and ovigerous females) when exposed to planktivorous predators. In addition, we could not detect any significant difference in the capture success of larval sea bass when feeding on the different reproductive stages of *E. affinis*. We further demonstrated that size and behavior were two major underlying mechanisms responsible of enhanced conspicuousness of *E. affinis* ovigerous females to larval sea bass.

4) As regards turbulence effects on the feeding rates, we observed different patterns depending on the prey type. First, when feeding on a non-evasive prey (*Artemia* sp.) offered at realistic densities, no dome-shaped relationship could be observed and

increased turbulence levels had negative effects on the ingestions rates of both larvae and juveniles of sea bass. However, when feeding on an evasive prey (*E. affinis*), a dome-shaped relationship was observed, with intermediate turbulence being beneficial to planktivorous fish. This discrepancy warrants the need to differently address the effects of turbulence on planktivorous fish foraging efficiency depending on the prey type (*i.e.* non-evasive or evasive).

5) Increasing turbulence resulted in decreased maximum food intake levels in larval sea bass. The implications of this result are twofold. First, they demonstrate the need to carefully choose the exposure duration while designing predation experiments under turbulence. Second, they reveal the necessity to parameterize bio-physical coupling models with different feeding thresholds, depending on flow conditions in order to avoid overestimating the benefits of turbulence.

6) When offered dead and live copepods separately, juveniles of sea bass preyed more intensively on live prey, irrespective of the turbulence level. This suggests that sea bass juveniles are able to discriminate copepods' active behavior from copepods' passive turbulence-advection.

More generally, this study shows how both plankters' behavior and turbulence can influence the range of food resources available to fish larvae (*i.e.* trophic niche breadth). In fact, with a comparable size range, an evasive prey will not be as available to the predator as a non-evasive one. Similarly, a highly evasive prey, that is inaccessible to a predator in calm water conditions, may become more accessible under moderate turbulence.

8.2 Future research directions

Our study unveiled the importance of investigating planktonic predators' search patterns on both vertical and horizontal projections. This can be applied on existing databases. In fact, numerous authors reported empirical results of 3D behaviors of planktonic organisms. Among these reports, very few tested for the isotropy of the swimming behavior. A reassessment of these databases, based on a comparison of vertical and horizontal projections, will undoubtedly cast light on how plankter's behavior is affected by gravity.

Complexity of the swimming path affected the outcome of the predatory sequence of whitefish larvae. If this observation is verified for other species, special care should be taken when theoretically assessing predator-prey interactions under an optimal foraging theory (Stephens and Krebs, 1986) framework. Future experimental effort could therefore be oriented toward the investigation of the effects of swimming complexity on the capture success in the most commonly investigated temperate fish species such as Atlantic herring (*Clupea harengus*), Atlantic cod (*Gadus morhua*) and sprat (*Sprattus sprattus*). The results of such investigations could provide modelers with better parameters to fine-tune existing models for these species (*e.g.*, Pitchford *et al*., 2003; Galbraith *et al*., 2004).

Prey swimming properties affected the feeding rates of fish larvae. The perceptive area of a predator may accordingly be considered of variable geometry depending on prey swimming patterns. Incorporating such variability into predator-prey encounter models could indeed give us new insights on how changes in foraging ground characteristics (*i.e.* changes in prey composition) can affect larval foraging success.

Despite the higher vulnerability of ovigerous females of *E. affinis* to predation, this species is one of the dominant copepods in the Seine estuary. We hypothesized that the viability of its eggs following a passage through the gut of larval fish (Flinkman *et al.*, 1994; Conway *et al.*, 1994) could explain *E. affinis* success in the natural environment. Future experiments, testing whether *E. affinis* nauplii can emerge from incubated feces of fish larvae collected *in situ* during spring, are warranted to validate this hypothesis.

In our study, we investigated the effect of turbulence on planktivorous fish ingestion rates. This process integrates the effects of turbulence on the whole predator-prey interaction sequence. In order to determine the effects of turbulence on each step of the predator-prey sequence, video recordings can be used. Namely, videos can help elucidate whether turbulence reduces the escape abilities of copepods yielding higher capture success at intermediate turbulence.

Sea bass juveniles consistently preyed more intensely on live than on dead copepods. Video recordings of the feeding behavior on live and dead prey offered independently would be suitable to resolve the underlying mechanisms of this observation.

In summary, the results of this dissertation reveal the existence of hitherto neglected effects of behavior and turbulence on the predator–prey interactions in the plankton. Future modelling studies taking into accounts parameters such as anisotropy of larval fish search patterns, effects of plankters' swimming behavior on capture and encounter rates, and differential effects of turbulence depending on prey type, could be complementary to this study.

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