

CHAPITRE 2

THE EFFECT OF TURBIDITY ON THE FEEDING ABILITY OF JUVENILE WINTER FLOUNDER (*Pseudopleuronectes americanus*, Walbaum)

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CHAPITRE 1

INTRODUCTION GÉNÉRALE

1.1 Biologie de l'espèce

1.1.1 Généralités

La plie rouge, *Pseudopleuronectes americanus* (Walbaum, 1792), est un poisson plat de la famille des Pleuronectidae (Scott & Scott, 1988) qui vit le long de la côte Atlantique du continent Nord Américain. Cette espèce se retrouve principalement le long des côtes du Labrador jusqu'à la Géorgie (Bigelow & Schroeder, 1953, Pereira et *al.*, 1999) et dans le sud du golfe du Saint Laurent (Division 4T de l'OPANO). Elle vit sur des fonds meubles à modérément durs et ne dépasse que très rarement des profondeurs avoisinant les 40 m (McCracken, 1963; Scott & Scott, 1988). Cette espèce semble montrer un patron de migration saisonnier assez complexe. Dans l'estuaire du Saint-Laurent, au printemps, la plie rouge se retrouve dans la zone intertidale principalement dans le but de s'y reproduire, mais également pour y trouver une abondante nourriture (Vaillancourt et *al.*, 1985). En revanche, au cours de l'été, elle s'éloigne des côtes pour vivre à des profondeurs comprises entre 20 et 40 m en hiver. De plus, la plie rouge produit des protéines antigels capables d'empêcher l'apparition de cristaux de glace dans le liquide interstitiel (Fletcher, 1977) la rendant ainsi apte à survivre à de basses températures (-1,5°C). Cette répartition saisonnière

semble être dictée par les conditions thermiques locales, mais également par la disponibilité en nourriture (Tyler, 1971). Le régime alimentaire de la plie rouge est de type omnivore ou opportuniste, celle-ci s'alimentant principalement d'espèces de la macrofaune benthique. Cette espèce consomme une large variété de proies telles que des polychètes (Linton, 1921), des amphipodes, des mollusques (Vaillancourt, 1982), mais également des œufs de capelan (Kennedy & Steele, 1971; Frank & Leggett, 1983).

1.1.2 Maturation sexuelle et fécondité

L'âge à la maturation chez la plie rouge semble extrêmement variable le long des côtes canadiennes. La maturité sexuelle surviendrait vers 2 ans au Banc Georges contre une moyenne de 7 ans dans la région de Terre Neuve. Dans le golfe du Saint-Laurent, la maturité sexuelle serait atteinte à l'âge de trois à quatre ans (Pitt, 1990). Kennedy et Steele (1971) révèlent que la maturité sexuelle est plutôt dépendante de la taille du poisson que de son âge. Toutefois, Beacham (1982) rapporte l'extrême variabilité de cette maturation d'année en année. La plie rouge est une espèce très féconde, avec un nombre moyen d'œufs par femelle de 500 000 (Scott & Scott, 1988). Néanmoins, la fécondité varie également le long des côtes, avec des moyennes allant de 99 000 à 2 millions d'œufs pour des longueurs variant de 220 à 440 mm à la hauteur de Terre Neuve (Kennedy & Steele, 1971) contre 435 000 à 3.3 millions d'œufs pour des longueurs avoisinant les 300-450 mm le long des côtes du Massachusetts (Topp, 1968).

1.1.3 Les stades de développement : œufs, larves et juvéniles

Les œufs, de petite taille (diamètre compris entre 740 μm et 850 μm), se déposent au fond et adhèrent aux roches et à la végétation (Breder, 1923; Pitt, 1990). Ceux-là éclosent après une période d'incubation d'environ 80 degrés-jours en laboratoire (Litvak, 1999). À leur naissance, les larves pélagiques présentent une symétrie bilatérale, des yeux et un corps non pigmentés. Durant les premiers jours, elles se nourrissent grâce à leurs réserves énergétiques présentes dans le sac vitellin, puis passent à une alimentation exogène (Sullivan, 1915). Le stade larvaire s'achève avec la métamorphose, qui intervient en milieu contrôlé à environ plus ou moins 44 jours après l'éclosion à une température de 10°C (Ben Khemis et *al.*, 2003). Scott et Scott (1988) rapportent que les larves dérivent durant 2 à 3 mois dans les eaux de surface avant la métamorphose. La métamorphose se caractérise par la migration de l'œil gauche vers le côté droit de la tête (Specker et *al.*, 1999) ainsi que par l'aplatissement du corps avec un changement d'orientation de 90° (Ballard et *al.*, 1987). La métamorphose entraîne des modifications morphologiques qui sont associées à la phase de transition entre la vie pélagique et la vie benthique. Ce changement d'habitat induit alors des changements comportementaux ainsi que des modifications du régime alimentaire (Yamashita et *al.*, 2001) qui nécessitent de nombreuses adaptations anatomiques et métaboliques. Tanaka et *al.* (1996) rapportent la formation, durant cette période, de glandes gastriques, de caeca pyloriques, ainsi que la transformation de l'épithélium oesophagien, l'élargissement de la vésicule biliaire et l'involution hépato-pancréatique chez la plie japonaise *Paralichthys olivaceus*. Une période de jeûne, d'environ 2 jours pour la plie

japonaise (Tanaka et *al.*, 1996), semble nécessaire pour la réorganisation fonctionnelle du système digestif au vue d'une alimentation benthique. Le changement d'habitat qui suit la métamorphose semble également provoquer un important bouleversement d'ordre écologique. Une fois la métamorphose terminée, la plie rouge atteint alors le stade juvénile.

1.2 Mise en contexte

1.2.1 État actuel des stocks

Dans l'estuaire maritime et le golfe du Saint-Laurent, la plie rouge contribue à des pêches localisées, fournissant ainsi les pêcheurs de homard en appâts et dans l'approvisionnement des marchés limités de consommation. La plie rouge est également capturée accessoirement dans la pêche à la morue, à la merluche blanche et à la plie canadienne. Cependant depuis le moratoire sur la morue, elle a fait l'objet d'une pêche dirigée (MPO, 2003). Depuis 1997, la plie rouge, la limande à queue jaune ainsi que la plie canadienne sont gérées en fonction d'un total autorisé de captures dans la région des Maritimes (Stobo et *al.*, 1997). La plie rouge constitue cependant le gros des débarquements. De plus, selon les pêcheurs, l'abondance des poissons plats dans cette zone est très faible et les données scientifiques laissent entrevoir une diminution des poissons de grande taille et une baisse de recrutement (Stobo et *al.*, 1997). Les données de débarquements de plie rouge (MPO, 2003) indiquent une diminution d'environ 200 tonnes de 2001 à 2002, passant ainsi de 600 à 400 tonnes. Les relevés du MPO notent également

une diminution de la taille et de la masse chez la plie rouge. Toutefois, les informations sur l'abondance de la plie rouge semblent critiquées par l'industrie, puisqu'elles ne couvrent pas tous les habitats côtiers, ni le recrutement (MPO, 1999). La plie rouge est donc une espèce exploitée de façon importante (Stickney, 2000) si l'on tient compte des pêches récréatives, commerciales et des prises accessoires.

1.2.2 Le potentiel aquacole de la plie rouge

Dans les Maritimes, la production aquicole est principalement basée sur la production de mollusques, avec l'implantation de sites d'élevages consacrés aux moules et aux pétoncles. L'industrie sur la côte ouest canadienne est très diversifiée avec la production de différentes espèces de mollusques et de salmonidés dont le saumon atlantique (*Salmo salar*). L'industrie piscicole, soumise à une importante concurrence internationale depuis quelques années (Litvak, 1996), a dû se diversifier et développer de nouveaux secteurs de production.

La production annuelle maricole au Québec maritime est loin d'atteindre celle de l'aquaculture en eau douce (2 000 tonnes métriques) (MAPAQ, 2000). La plie rouge a été désignée comme une espèce prometteuse et économiquement viable pour l'industrie piscicole au Canada Atlantique (Litvak, 1994; 1996). C'est une espèce eurytherme et euryhaline (Pearcy, 1961; Litvak, 1999) très bien adaptée aux conditions extrêmes survenant en hiver le long des côtes canadiennes. Comme mentionné précédemment, elle



possède des protéines antigel plasmatiques qui lui permettent de résister à des températures aussi faibles que $-1,5^{\circ}\text{C}$ (Duman & De Vries, 1974; Fletcher, 1977). D'autre part, la plie rouge ne supporte pas les températures avoisinants les 20°C , ce qui la rend ainsi inappropriée pour les industries piscicoles d'Amérique latine et du sud. Enfin, la plie rouge est aussi une espèce dont la valeur marchande est élevée et semble très comparable à celle d'autres espèces de poissons, tel que le saumon Atlantique (National Marine Fisheries Service's - Fishery Market News, 2005).

1.3 Problématique

1.3.1 Les études antérieures

Dans les années 1970, différentes études se sont intéressées à la plie rouge et ont été consacrées particulièrement à l'ovulation des femelles, au frai, au traitement des œufs et aux conditions d'incubation (Smigielski & Arnold, 1972). Ensuite, les études ont été principalement axées sur le succès reproducteur, la croissance et le métabolisme des larves (Laurence, 1975; Buckley, 1982; Klein-MacPhee *et al.*, 1982; Buckley *et al.*, 1991). En 1994, Litvak fait l'ébauche d'une technique d'élevage de larves de plie rouge et ce, dans une optique aquacole, qui sera ensuite améliorée par Lee et Litvak (1996). Toutefois, beaucoup d'autres techniques restent à mettre au point et particulièrement le passage du stade larvaire à celui de juvénile, qui reste encore très difficile à maîtriser. Une étude de Ben Khemis *et al.* (2000) réalisée dans notre laboratoire, a été menée sur différents régimes

alimentaires afin d'optimiser l'élevage larvaire. Les études de Seychelles (2002) et De Montgolfier (2003) sur des juvéniles en début de phase benthique ont démontré la présence d'une phase critique lors du passage à la vie benthique suivie d'un pic de mortalité survenant environ 3 semaines après la métamorphose. L'hypothèse la plus probable pouvant expliquer cette forte mortalité serait la disponibilité alimentaire. D'autres facteurs pourraient être à l'origine de ces fortes mortalités, dont notamment l'absence de substrat sédimentaire dans les bassins d'élevage. En effet, les travaux de Seychelles (2002) et de Montgolfier (2003) ont été réalisés dans des bassins « à fond nu », soit sans couche de sédiment. Étant donné que les juvéniles montrent des comportements d'enfouissement dans le sédiment aussi bien en laboratoire (Moles & Norcross, 1995) qu'en milieu naturel (Phelan et *al.*, 2001), il serait plus que probable que la présence de substrat ait une influence sur la survie et la croissance des juvéniles (Joly, 2004). Joly (2004) a comparé l'impact de différents types de substrats sur la croissance des juvéniles de plie rouge et ce à 2 sites expérimentaux différents. Les taux de croissance des juvéniles variaient cependant en fonction du site, malgré l'utilisation d'un protocole expérimental similaire. D'après Joly (2004), le site ayant la meilleure croissance présentait une teneur assez élevée de sédiments en suspension.

1.3.2 La turbidité

Plusieurs études démontrent l'effet néfaste de la turbidité sur le succès d'alimentation de différentes espèces de poissons et spécifiquement chez les salmonidés (Sigler et *al.*,

1984; Berg & Northcote, 1985). En effet, les particules en suspension peuvent avoir des effets délétères sur leur taux d'alimentation, leur croissance et leur survie (Newcombe & MacDonald, 1991; Gregory & Northcote, 1993). Le principal effet de la turbidité est de diminuer la pénétration de la lumière dans le milieu ainsi que d'affecter l'atténuation spectrale (McFarland, 1986) et par conséquent d'entraîner une cécité visuelle (Vinyard & O'Brien, 1976; Noggle, 1978; Gardner, 1981). Plusieurs espèces, incluant la plie rouge, sont des prédateurs chassant à vue et sont alors grandement dépendants de la lumière pour détecter et consommer leurs proies (Able et *al.*, 1999). Ainsi, une augmentation de la turbidité influencerait les conditions lumineuses du système et, par conséquent, le succès d'alimentation des juvéniles. Frame (1971) rapporte que la quantité et la durée d'alimentation chez la plie rouge sont principalement fonction de l'intensité lumineuse. De plus, une teneur anormalement élevée de particules en suspension pourrait réduire le volume de recherche ou la distance de réaction entre un prédateur et sa proie (Gardner, 1981; Berg & Northcote, 1985; Barrett et *al.*, 1992) altérant ainsi le taux de rencontre et donc les probabilités d'attaques (O'Brien, 1987; Miner & Stein, 1996). La dispersion de la lumière engendrée par les particules en suspension diminuerait également le contraste entre un objet et son arrière plan, entraînant ainsi une diminution de la visibilité de l'objet (Antony, 1981; Aksnes & Giske, 1993; De Robertis et *al.*, 2003).

1.4 Les objectifs

Dans une perspective environnementale, il est nécessaire de comprendre les différents facteurs affectant les plus jeunes stades chez la plie rouge en vue du futur recrutement. En

effet, les différents facteurs environnementaux comme la température, la salinité, la photopériode ou encore la turbidité peuvent avoir des effets sur la survie et la croissance chez la plie rouge. L'objectif de ce projet était donc de déterminer les effets de la turbidité sur l'alimentation des juvéniles de plie rouge suivant des niveaux croissants de turbidité. Par ailleurs, la compréhension de ces effets sur l'alimentation reste plus que cruciale quand à la détermination du succès de recrutement dans les aires nourricières.

CHAPITRE 2

THE EFFECT OF TURBIDITY ON THE FEEDING ABILITY OF WINTER FLOUNDER (*Pseudopleuronectes americanus*, Walbaum)

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ABSTRACT

In North America, the decline in many native flatfish stocks, including winter flounder (*Pseudopleuronectes americanus*), has been attributed to overfishing, starvation, and habitat loss or alteration. Increased suspended sediments have been associated with reduced spawning, feeding, growth, and recruitment. In this study, we examined the effects of turbidity on the feeding behaviour of juvenile winter flounder. Juveniles were exposed to different turbidity levels (0 to 352.5 NTU) for short periods of time (4 hours) and fed with 24-hour-old brine shrimp nauplii (*Artemia* sp.). In each trial, we evaluated the percentage of fish that were feeding and used image analysis to evaluate stomach contents. The different levels of turbidity did not modify the percentage of juveniles feeding or the area of the digestive system filled with brine shrimp nauplii. However, the IOD index (area of stomach filled with nauplii x stomach-content colour intensity) was lower in juveniles feeding in a turbid environment than in those not exposed to turbidity. This was a presence–absence response, as the index did not vary with the intensity of turbidity. Overall, water turbidity had no major impact on the ability of winter flounder juveniles to capture live prey.

2.1. Introduction

Winter flounder, *Pseudopleuronectes americanus* Walbaum, inhabit relatively shallow waters in the northwest Atlantic from Labrador to Georgia (Bigelow and Schroeder, 1953, Scott and Scott, 1988; Pereira et al. 1999). Winter flounder, with the exception of the population on Georges Bank and Nantucket Shoals, use estuaries as their primary spawning sites and nursery habitats (Howe et al., 1976; Pierce and Howe, 1977, Able and Fahay, 1998). Spawning of demersal eggs occurs during winter and early spring (Saila, 1961; Pearcy, 1962; Crawford and Kerry, 1985; Scarlett, 1991; Phelan, 1992; Stoner et al., 1999). After hatching, pelagic larvae remain in the water column for approximately 60 days (Laurence, 1975; Chambers and Legett, 1987; Keller et al. 1999), with larval life duration being strongly dependent on water temperature (Chambers et al., 2001). Like other flatfish species, winter flounder settle on the sea bottom following metamorphosis to the juvenile stage (eye migration, vertical rotation imposture) (Percy, 1962; Tanaka et al., 1989; Tanaka et al., 1996; Chant et al. 2000).

Estuaries provide an abundance of food, favourable temperatures, and shelter from predation (Karakiri et al., 1991; Van der Veer and Witte, 1993; Berghahn et al., 1995; Gibson, 1999; Reichert et al., 2000). However, these nursery areas generally show a high concentration of suspended sediments (Witting, 1995; Able and Fahay, 1998).

The biomass of winter flounder stocks has recently declined and the potential causes are principally overfishing (MPO, 2003). In other fish species, alteration and loss of habitat have also been identified as other causes of population decline (Gregory and Levings, 1998; Rowe and Dean, 1998; Rowe et al., 2002). Turbidity can also affect the survival rate of fish by decreasing habitat quality (Duarte et al., 1986; Goldsborough and Kemp, 1988) and by reducing growth through a diminution in food supply or feeding success (Yamashita et al., 2001). Turbidity brings about these effects by reducing illumination and visual clarity (Vinyard and O'Brien, 1976; Noggle, 1978; Gardner, 1981) and by affecting spectral attenuation (McFarland, 1986). Many species including winter flounder are visual feeders and thus are highly dependent on light to efficiently detect and consume their prey (Able et al., 1999; Ryer and Olla, 1999). Hence, an increase in turbidity influences light conditions and may also affect juvenile fish feeding success. Frame (1971) noted that the amount and duration of feeding vary with light intensity. Moreover, a high level of turbidity can reduce the reactive distance between a predator and its prey by reducing visual clarity (Gardner, 1981; Berg and Northcote, 1985; Barrett et al., 1992). It may also alter the prey encounter rate, pursuit, and/or attack probabilities (O'Brien, 1987; Miner and Stein, 1996). Light scattering by suspended sediments reduces the apparent difference in brightness between an object and its background and consequently the visibility of that object (Antony, 1981; Loew and McFarland, 1990; Aksnes and Giske, 1993; De Robertis et al., 2003). Understanding the role of environmental factors, such as turbidity, on feeding success and growth of juveniles in nursery areas may be crucial for the determination of their recruitment success (Tanaka et al., 1989).

In this study, we examined the effects of turbidity on the feeding success of juvenile winter flounder. Feeding ability and feeding behaviour of winter flounder juveniles in different turbidity levels were determined by examining food ingestion under laboratory conditions. We interpreted our results in relation to the characteristics of the natural habitat of winter flounder.

2.2 Materials and methods

2.2.1 Fish collection and holding conditions

Winter flounder larvae were reared in the facilities of the Station aquicole de Pointe-au-Père, Québec, using the protocol described by Ben Khemis et al. (2000). Following settlement, the juveniles were transferred to the Maurice Lamontagne Institute (Department of Fisheries and Oceans, DFO, Mont-Joli, Qué., Canada) where the experiments took place. Fish were held in rectangular tanks provided with a continuous flow of aerated seawater and a clay substratum. Water temperature was maintained at 10°C ($\pm$ 2°C) and the salinity ranged from 26 to 29‰. The photoperiod was set at 16L:8D with fluorescent lights at an intensity of 375 $\mu\text{mole quanta.m}^{-2}.\text{s}^{-1}$. Juveniles were acclimated to laboratory conditions for a minimum of 3 days prior to experimentation and fed with live *Artemia* sp. nauplii twice daily at 9:00 and 15:00 respectively. Prior to the experiments, juvenile winter flounder were starved for 16 hours. Preliminary tests revealed that this duration was sufficient to eliminate the presence of prey from the digestive system. The size of the juveniles used in the experiments varied from 6.4 to 12.2 mm in total length (TL).

2.2.2 Turbidity

In order to test the influence of turbidity on juvenile feeding success, different turbidity levels ranging from 0 to 353 NTU were studied. The highest turbidity level was selected to represent high levels occurring during storms in natural conditions. Feeding

experiments were conducted in a series of seven identical glass aquaria (31x13x20 cm) containing 4L of seawater mixed with 125 ml of kaolin clay suspension (Figure 1). A perforated Plexiglas plate was fixed hermetically at 3.5 cm from the bottom (Figure 2). Four additional holes (15.7 mm in diameter) 2 cm from each corner were fitted with Plexiglas tubing for aeration. Apertures were closed with 150 μ m nitex to avoid loss of prey under the bottom plate. This system allowed upwelling water circulation and good suspension of the clay particles.

Turbidity was generated by mixing predetermined amounts of kaolin clay 24 h prior to the experiments to obtain stable turbidity levels. Despite identical kaolin concentrations, it was not possible to obtain identical turbidity levels among aquaria. Thus, a turbidity measurement was done in each aquarium at the beginning and after completion of the feeding experiments and the average measurement was used to indicate the tested turbidity level in each aquarium. Turbidity was measured using an HF DRT-15CE turbidimeter (HF Scientific Inc., Ft. Myers, FL) and expressed in nephelometric turbid units (NTU, Apha, 1985). Measurements were done at mid-water and in the center of the aquariums following preliminary trials that indicated similar turbidity levels everywhere in the test aquariums. Water temperature and salinity were verified daily with a hand-held electronic device (WTW LF 333, Canada wide).

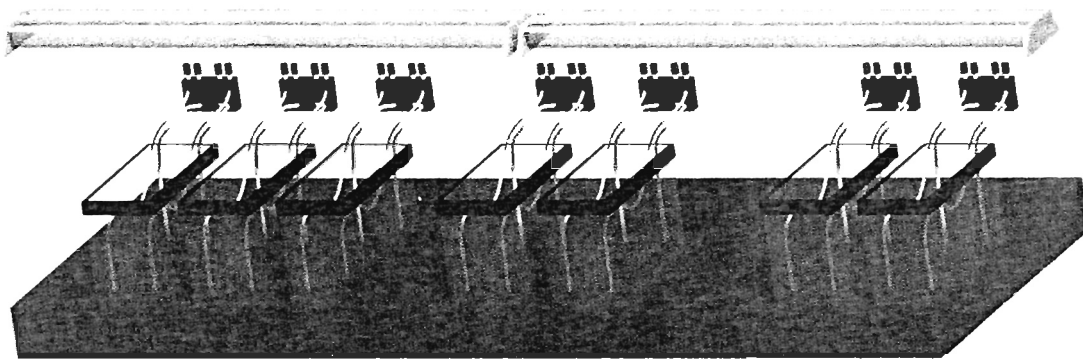


Figure 1. Series of seven identical glass aquariums used for the experiments.

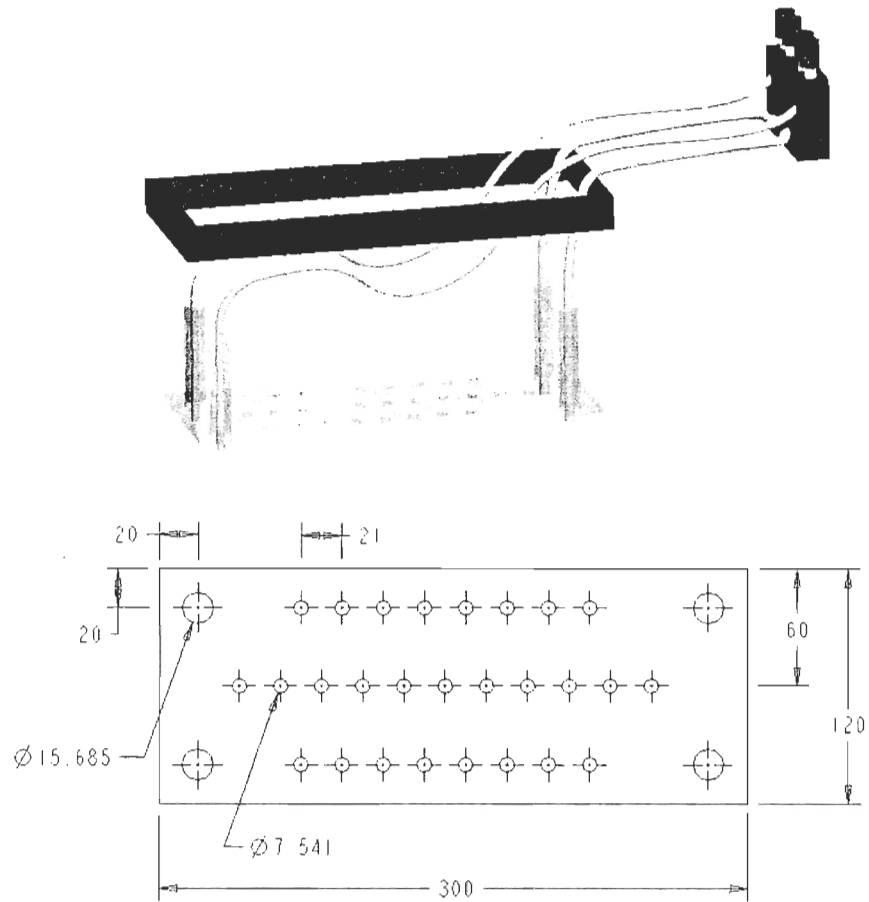


Figure 2. Example of air lift system inserted in each aquaria to generate suspension of clay particles.

2.2.3 Experimental apparatus

For each trial, a group of ten juveniles was introduced to an aquarium. The juveniles were arbitrarily chosen each day and examined to insure that their digestive system was empty. Pictures of these individuals were also taken. For each trial, the starved juveniles were introduced into each test aquarium at 8:30 and acclimated for 30 min before the introduction of live brine shrimp nauplii (*Artemia* sp.).

We performed a series of preliminary investigations to determine the prey size and density to use. Trials were conducted with 24h old nauplii because their pink colouration allows easy visualization of their presence in the juvenile's digestive system. Fifteen thousand nauplii were introduced to each aquarium, resulting in approximately 3636 individuals per litre. In the day, prey were introduced at the water surface of each aquarium with minimal water disturbance. The feeding period lasted 4 hours after which experiments were terminated. Juveniles were then gently captured and pictures were quickly taken for further image analysis.

The different kaolin concentrations used to produce the different turbidity levels were randomly used in the aquariums on the different days of the experiment. Tested fish were only used once for the first 21 trials. However, due to the limited number of fish, juveniles were used more than one time in the other trials. Juveniles that had been used for trials were placed in a different holding tank for a minimum of 3 days before being used in subsequent trials. Feeding experiments took place in 3 to 7 aquariums at a time.

2.2.4 Image analysis

Images of juveniles were taken with a digital camera mounted on a microscope (LEICA, MZ75) and exported to an image analysis software (Image Pro-plus 5.0, Media Cybernetics, Silver Springs, MD). Due to differences in the light intensity of the background, each image was standardized before measurements were taken to allow reliable comparisons. Representative and similar zones among pictures were used to make the standardization. Each image was constituted of several pixels that ranged in value between 0 and 256, representing respectively low and high light transmission levels. The lowest light transmission level was determined in the darkest area of the picture, whereas the highest level was measured arbitrarily between the 18th and 19th fin rays of the dorsal fin, where the light could pass easily through. This method allowed the calibration of the background intensity of each picture. A further calibration was done with the software to take into account the magnification.

We used five parameters to characterize and quantify feeding success: total length (TL) and width of fish; total area of the coelomic cavity, and area of the digestive system filled with food, mean density, and integrated optical density of the food-filled area (IOD). The influence of turbidity on the feeding ability of juvenile winter flounder was determined by the number of feeding juveniles in each aquarium, the area of the digestive system filled with food for each juvenile (Figure 3), and an index calculated as the area of the digestive system filled with food multiplied by the colouration intensity (IOD index). The IOD variable allowed the distinction between similarly sized filled areas showing different

colouration intensity, with a dark colouration indicating a higher feeding content than light colouration (Figure 4). Dead juveniles, even if they had some stomach content, were excluded from the results. We had an average of ten fish per aquarium and the result for an aquarium was based on the average measurements from all live fish.

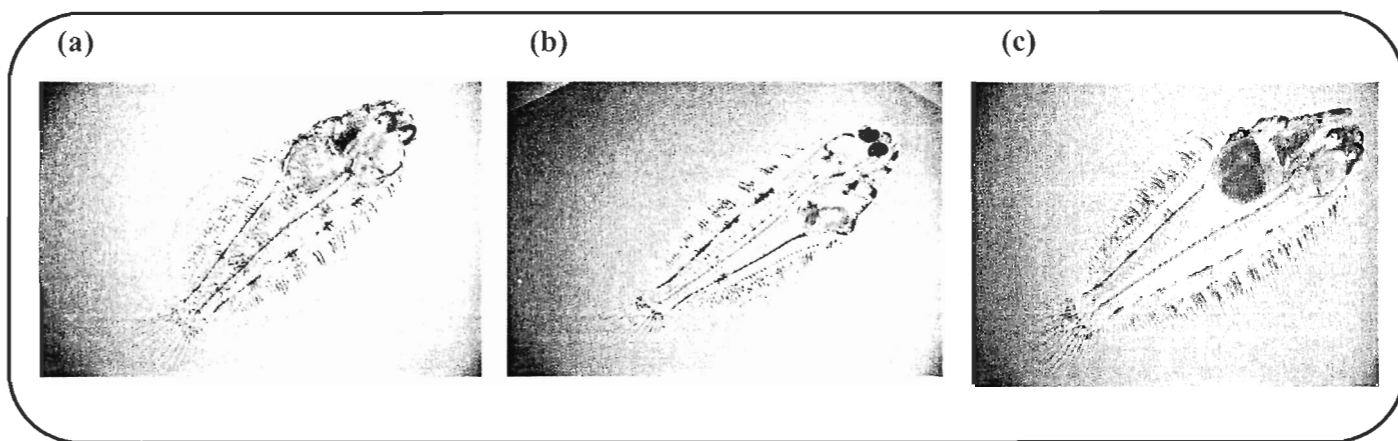


Figure 3. Juveniles winter flounder at different feeding levels: (a) starved juvenile (0%); (b) juvenile with 42% of the stomach and gut filled; (c) juvenile with 73% of the stomach and gut filled (magnification = 2x).

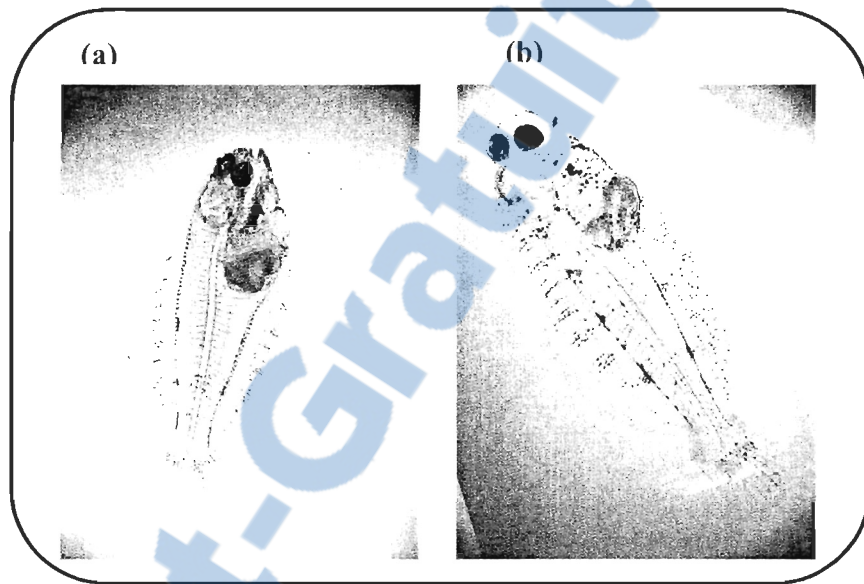


Figure 4. Two juvenile winter flounder showing a food-filled area of 54% but with different Integrated Optical Density indices (IOD): (a) IOD value is 0.41 (magnification = 1.6x); (b) IOD value is 0.19 (magnification = 2.5x).

2.2.5 Data analysis

Statistical analyses were done with the STATISTICA 6.0 software. The significance level used was $p < 0.05$. No data transformation was necessary to meet assumptions of normality (Kolmogorov-Smirnov test) or homoscedasticity (Levene test) for the different variables tested.

As the area of the digestive system could have been related to fish size, we tested the hypothesis of a relationship between fish size and the digestive system area using a linear regression test in clear water conditions. One-way ANOVAs were carried out to test the null hypothesis that mean percentage of feeding juveniles, percentage of food-filled digestive system, or IOD index were not affected by turbidity levels. If the ANOVAs indicated a significant treatment effect, a posteriori multiple comparison tests (LSD) were performed.

2.3 Results

The mortality rate was low, ranging from 3.3 to 18.33%, and was independent of the turbidity level. To evaluate the percentage of feeding juveniles, we did not take into account the dead fish in the total number and used a corrected average per aquarium (Table 1b).

Water turbidity, ranging from 0 to 353 NTU, did not affect the ability of juvenile winter flounder to capture live prey (ANOVA, $p = 0.76$, $df = 6$, $F = 0.55$; Figure 5a). At all turbidity levels, a high percentage of fish were feeding ($84\% \pm 16.03$; Table 1b). Moreover, turbidity had no effect on the percentage of the relative area of the digestive system containing food (Figure 5b) (ANOVA, $p = 0.14$, $df = 6$, $F = 1.74$). Nevertheless, in the absence of turbidity, the percentage of filled area was always above 20%, whereas we observed the lowest percentages when turbidity levels increased (Figure 6). On the other hand, turbidity had a significant effect on the IOD index (area of stomach filled with *Artemia* x stomach-content colour intensity) (ANOVA, $p < 0.01$, $df = 6$, $F = 1.26$). The highest IOD index was observed in the absence of turbidity, with an average of 0.37 ± 0.13 compared to 0.17 ± 0.08 in the presence of turbid water (Figure 7), but the intensity of turbidity had no further effect on this index.

We tested whether juvenile size (Table 2) could influence measurements in clear water conditions and found no significant relationship with the percentage of feeding fish ($r^2 = 0.24$, $p = 0.10$, $df = 1$, $F = 3.16$, $N = 12$; Figure 8a) or with the food content of the

digestive system ($r^2 = 0.04$, $p = 0.53$, $df = 1$, $F = 0.42$, $N = 12$; Figure 8b) for clear water conditions.

Table 1. Average percentage ($\pm$ SD) of feeding, non-feeding, and dead juveniles (a) and corrected percentages (dead fish not included) (b) during experimental trials at the different turbidity levels (in nephelometric turbidity units, NTU).

a)

<i>Turbidity (NTU)</i>	<i>Percentage of juveniles</i>		
	<i>Feeding</i>	<i>Non feeding</i>	<i>Dead</i>
0-46	91.66 $\pm$ 11.93	5.00 $\pm$ 6.74	3.33 $\pm$ 11.55
47-93	85.55 $\pm$ 8.82	6.66 $\pm$ 7.07	7.77 $\pm$ 8.33
94-140	73.33 $\pm$ 12.54	8.33 $\pm$ 11.69	18.33 $\pm$ 9.83
141-187	84.00 $\pm$ 18.66	10.00 $\pm$ 14.14	6.00 $\pm$ 13.42
188-234	80.00 $\pm$ 26.46	13.33 $\pm$ 15.27	3.33 $\pm$ 5.77
235-281	85.00 $\pm$ 13.78	10.00 $\pm$ 10.95	5.00 $\pm$ 8.37
282-353	90.00 $\pm$ 20.00	5.00 $\pm$ 10.00	5.00 $\pm$ 10.00
	84.22 $\pm$ 16.03	8.33 $\pm$ 10.84	6.96 $\pm$ 9.61

b)

<i>Turbidity (NTU)</i>	<i>Percentage of juveniles (only live fish considered)</i>	
	<i>Feeding</i>	<i>Non feeding</i>
0-46	95.00 $\pm$ 6.74	5.00 $\pm$ 6.74
47-93	92.97 $\pm$ 7.28	7.03 $\pm$ 7.28
94-140	93.98 $\pm$ 10.31	6.02 $\pm$ 10.30
141-187	90.00 $\pm$ 17.32	10.00 $\pm$ 14.14
188-234	84.17 $\pm$ 19.42	15.83 $\pm$ 19.42
235-281	89.40 $\pm$ 11.00	10.60 $\pm$ 11.00
282-353	93.75 $\pm$ 12.50	6.25 $\pm$ 12.50
	91.32 $\pm$ 12.08	8.52 $\pm$ 8.67

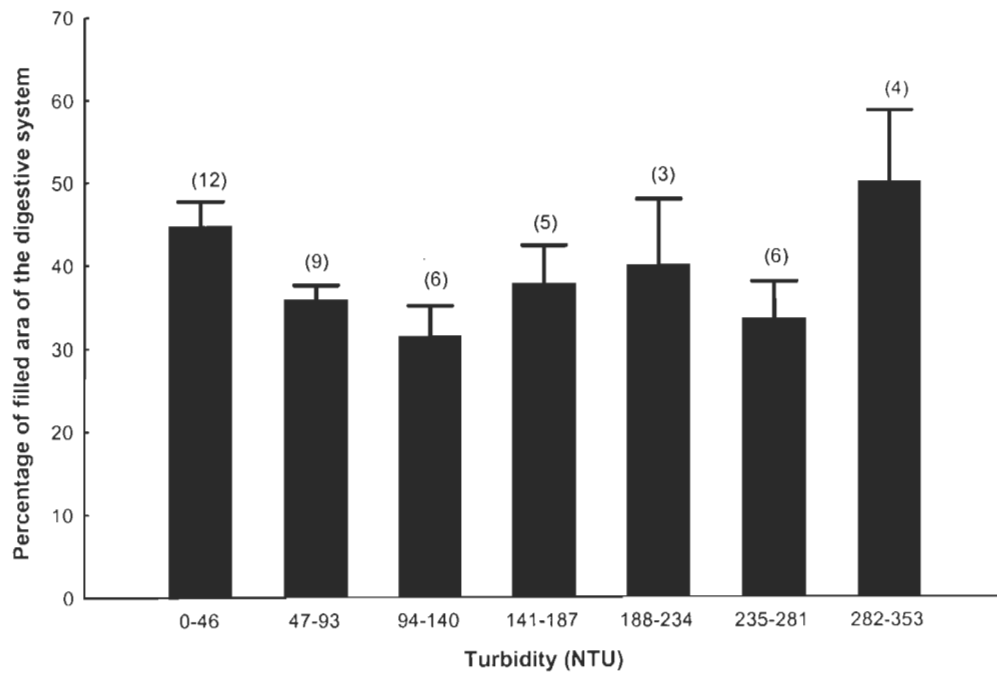
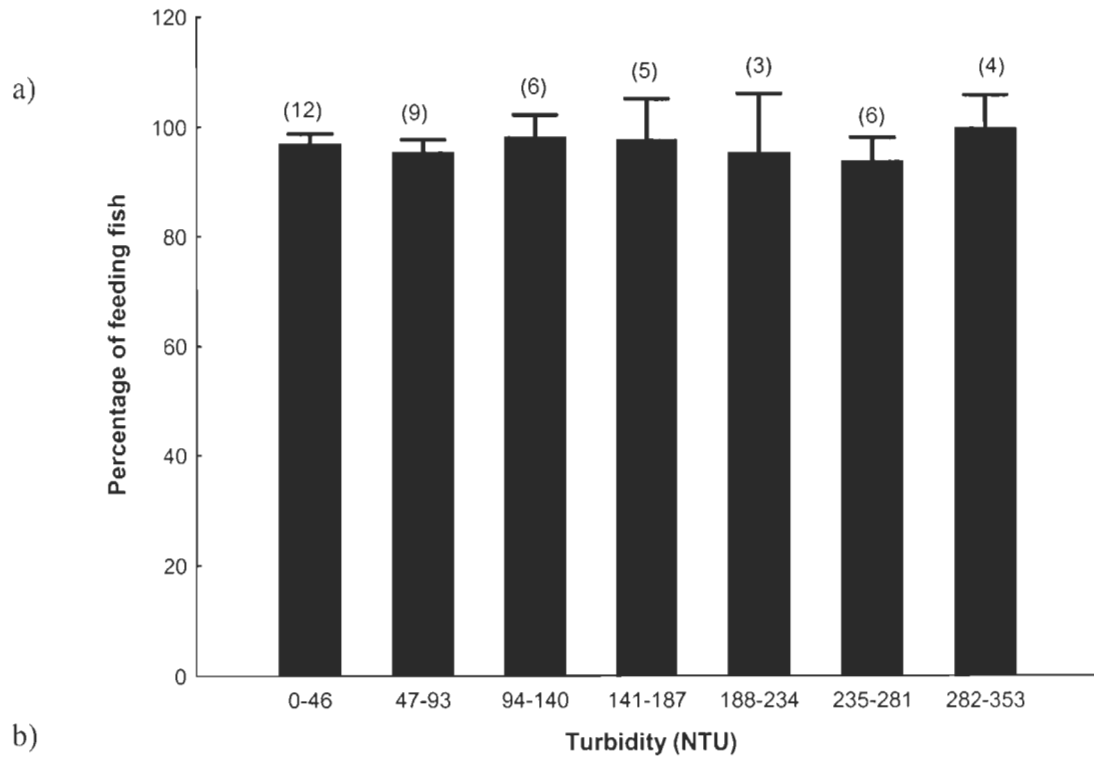


Figure 5. Effects of turbidity (in nephelometric turbidity units, NTU) on the percentage of feeding fish (a) and the filled area of the digestive system (b) in juvenile winter flounder fed *Artemia* sp. Mean $\pm$ SD, number of trials in parentheses.

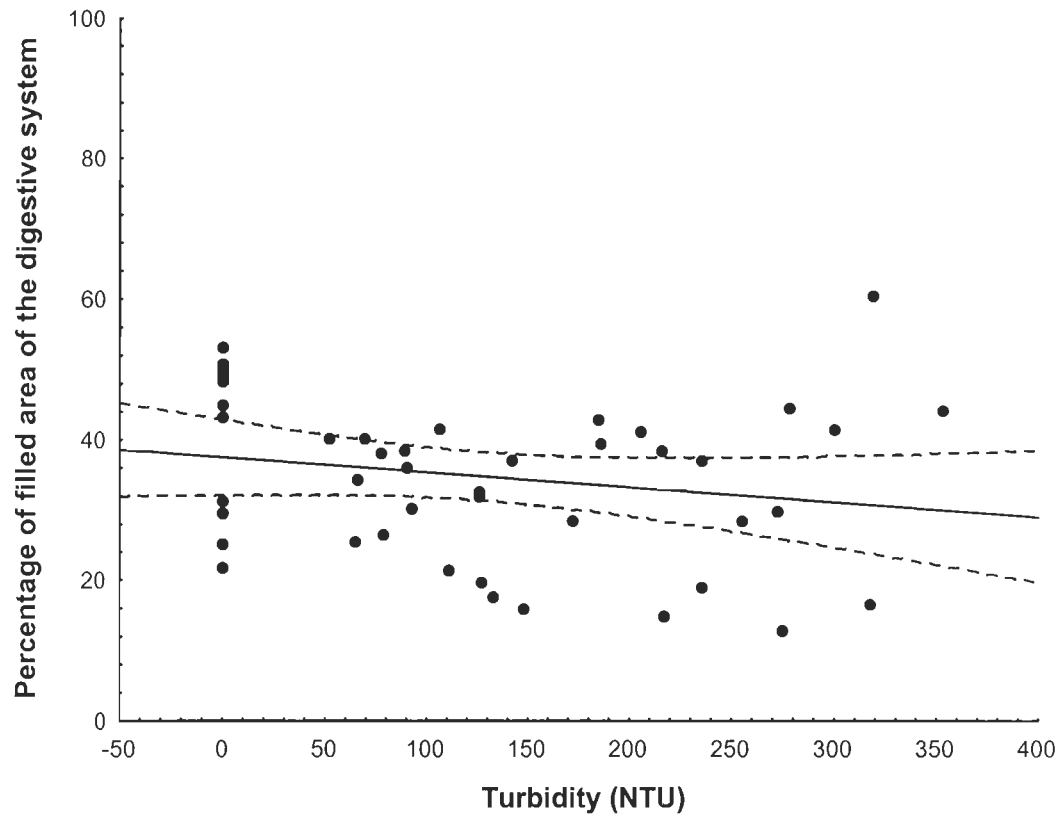


Figure 6. Effects of turbidity (in nephelometric units, NTU) on the percentage of filled area of the digestive system in juvenile winter flounder fed *Artemia* sp. Mean and 95% interval of confidence. Each point represents the mean value obtained from one experimental aquarium.

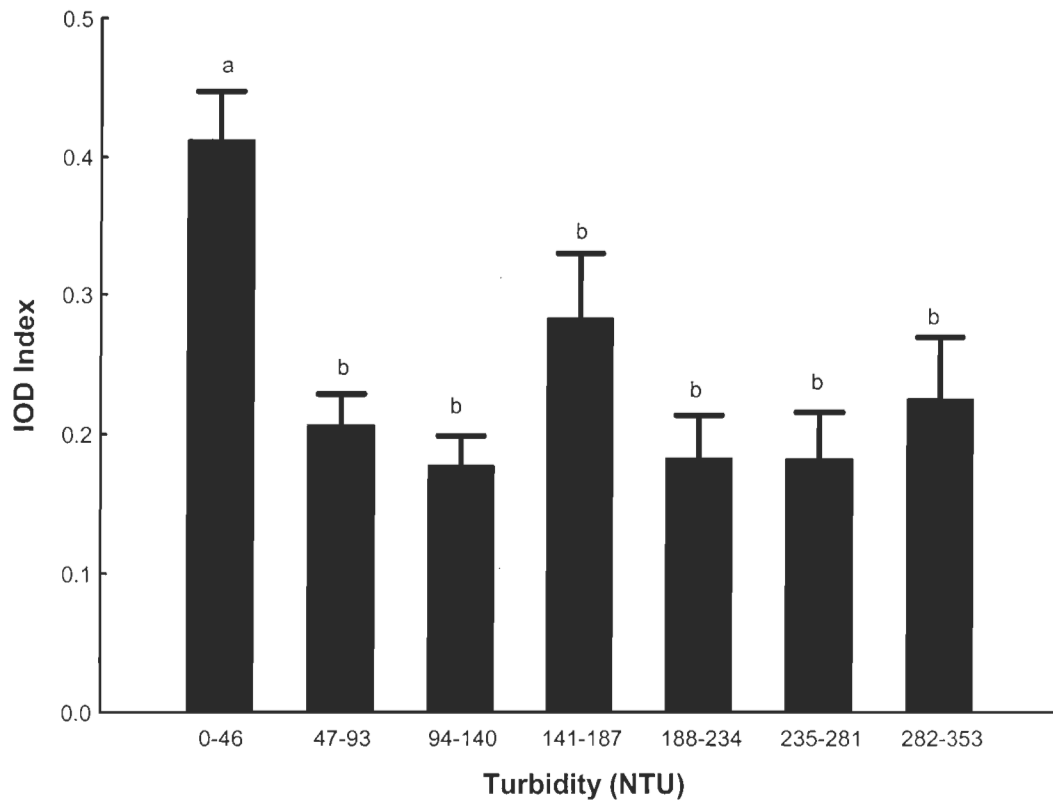


Figure 7. Effects of turbidity (in nephelometric turbidity units, NTU) on the Integrated Optical Density Index (% filled x colour intensity) in juvenile winter flounder fed *Artemia* sp. Mean and SD. Different letters indicate a significant difference among the treatments.

Table 2. Average total length and coelomic cavity area (mean $\pm$ SD) of juvenile winter flounder at six turbidity levels (in nephelometric turbidity units, NTU).

<i>Turbidity (NTU)</i>	<i>Total length (mm)</i>	<i>Coelomic cavity area (mm²)</i>
0-46	8.39 $\pm$ 0.35	1.55 $\pm$ 0.19
47-93	8.82 $\pm$ 0.33	1.68 $\pm$ 0.20
94-140	8.48 $\pm$ 0.28	1.48 $\pm$ 0.11
141-187	8.65 $\pm$ 0.32	1.64 $\pm$ 0.16
188-234	8.68 $\pm$ 0.23	1.62 $\pm$ 0.17
235-281	8.89 $\pm$ 0.31	1.71 $\pm$ 0.16
282-353	8.70 $\pm$ 0.46	1.63 $\pm$ 0.29

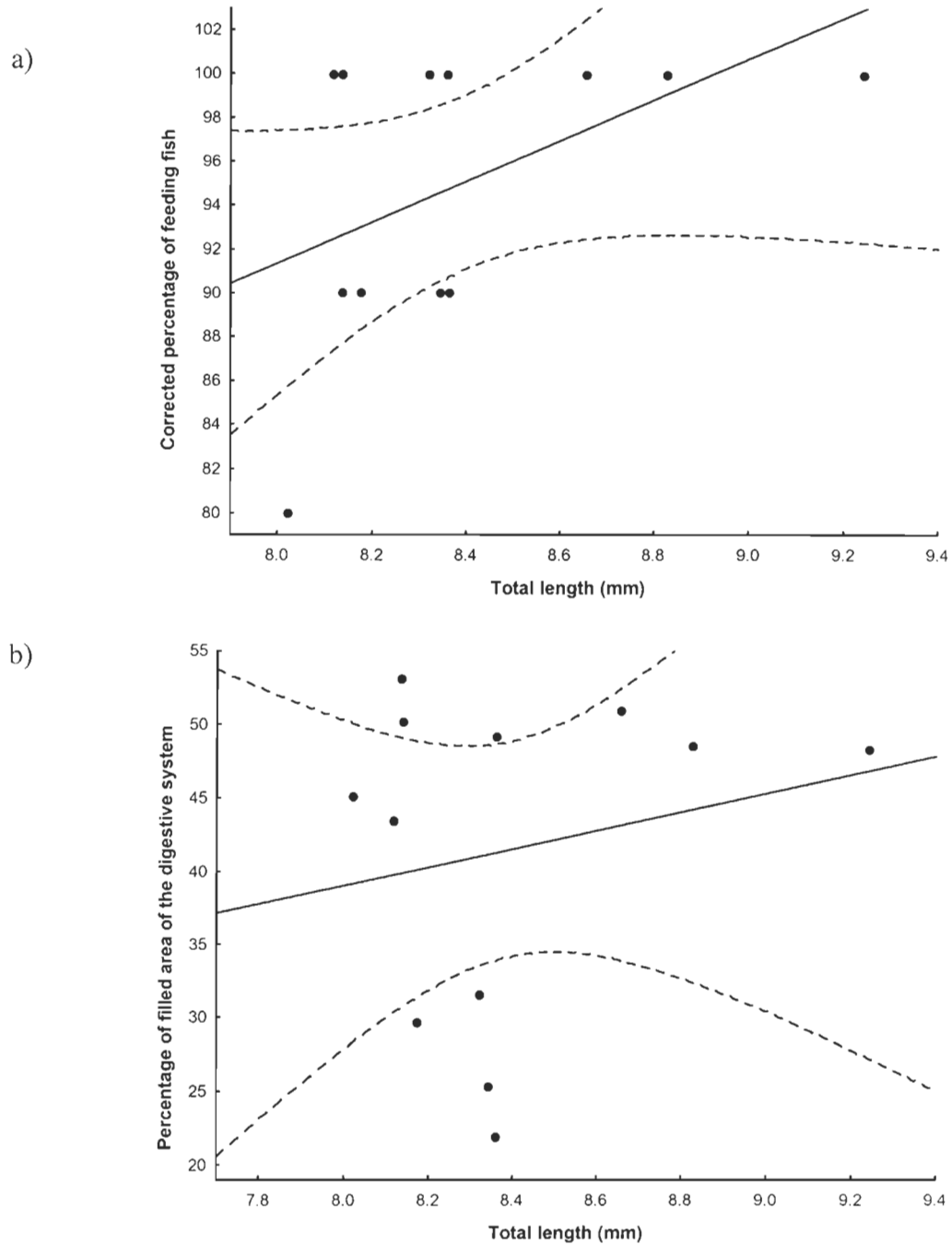


Figure 8. Effects of total length (mm) on the corrected percentage of feeding fish (a) and on the percentage of the digestive system that was filled in juvenile winter flounder fed *Artemia* sp.. Mean and 95% interval of confidence. Each point represents a mean per aquarium obtained during clear water conditions.

2.4 Discussion

Winter flounder are visual feeders (Laurence, 1977), with larvae that feed mostly on planktonic crustaceans and worms (Ross, 1991) and newly metamorphosed juvenile on copepod naupliis, small polychaetes, nemerteans, and ostracods (Pearcy, 1962). Following settlement, juveniles must develop specific adaptations to ensure feeding success in their new environment. A large increase in the retinal development results in increased photosensitivity in Japanese flounder during metamorphosis (Kitamura, 1990). In addition, studies on pelagic fish show similar specializations of the retina that enhance scotopic vision. Retinal rods of walleyes (*Stizostedion vitreum*) begin aggregating to form the macroreceptors (20-30 photoreceptors) when juveniles are between 60 and 70 mm, a size that coincides with the onset of the piscivory stage. This increasing visual acuity in dimly illuminated water is probably an additional advantage in the detection and capture of prey (Braekevelt et al., 1989). The *tapetum lucidum* appears during the first year of life and is fully developed in adult fish. The *tapetum* permits increased retinal sensitivity by reflecting light back onto the photoreceptors (Walls, 1967; Braekevelt, 1982). This adaptation to low light conditions is common among species that inhabit dimly lit environments (Braekevelt et al., 1989). In comparison to adaptations by pelagic fish, Omura et al. (2004) observed that photoreceptor cells in Japanese flounder, made up almost entirely of cone cells, first appeared in the retina at the age of 40 days, during metamorphosis. In contrast to this thin, single layer of cone cells, a thick, pseudo-multilayered arrangement of rod cells was found in the mature retina of the wild adults (Omura et al., 2004). The continuous increase in the number of rod cells in the flounder retina after metamorphosis also suggests an adaptation

to the benthic habitat and/or a nocturnal feeding behaviour (Kawamura and Ishida, 1986). Even though no studies have been conducted on the rod photoreceptor formation in winter flounder, we may hypothesize that winter flounder show a retinal development similar to that in Japanese flounder during their life history.

Our work did not indicate marked changes in the feeding success of juvenile winter flounder in different turbidity conditions. In pelagic fish, turbidity has often been considered to impair feeding behaviour and feeding success by decreasing visual feeding ability (*Lepomis macrochirus*, Gardner, 1981; *Oncorhynchus tshawytscha*, Gregory and Northcote, 1993). Gardner (1981) showed that turbidity levels (60, 120, and 190 NTU) had a significant effect on the mean total number of daphnia eaten per fish in bluegills (*Lepomis macrochirus*). For fish (75.3 mm), the mean number of daphnia consumed declined by almost 20% at 60 NTU to 50% at the highest turbidity level. Suspended sediment also modifies the foraging activities and visual ability in bluegills. The relationship observed between turbidity and the reaction distance of bluegills to daphnia prey declined log-linearly when turbidity increased (Vinyard and O'Brien, 1976). This situation was similar for juvenile chinook (*Oncorhynchus tshawytscha*) on *Artemia* prey (Gregory and Northcote, 1993) and for lake trout (*Salvelinus namaycush*) (Confer et al., 1978). Studies examining the effects of turbidity on the feeding of flatfish species are scarce. In contrast to our own results, Moore and Moore (1976) showed that turbidity reduced the ability of large European flounders (*Platichthys flesus*) to detect highly mobile epibenthic prey and increased the pursuit time before prey capture. Nevertheless, small flounders could detect *Asellus aquaticus* sp. of size 1.0 cm as efficiently as larger individuals regardless of the

turbidity (Moore and Moore, 1976). Moreover, they were able to find prey as small as 0.10 and 0.20 cm in clear and turbid water, respectively. Moore and Moore (1976) took into account the spatial distribution of prey in the water column, the degree of concealment by prey, the different degrees of motility and abilities to escape predation of prey species, and the turbidity. As small flounders could detect prey over a relatively large area, it is not surprising that the proportion of stomachs containing food remained high. Nevertheless, the degree of motility of different prey modifies the reaction distance and the encounter rate between predator and prey, which influence feeding success. The maximum distance that European flounder of all sizes could see *Gammarus pulex* and the time required to swim to the prey was identical to that of *A. aquaticus*, regardless of water conditions (Moore and Moore, 1976). However, fish were able to catch prey in only 80% of the *G. pulex* trials compared to 100% for *A. aquaticus*. For the highly motile *Eurydice pulchra*, flounders of all sizes were able to catch this prey only 3 to 4% of the times that it appeared within visual range. This study may presume that prey motility was the most important factor, decreasing the feeding ability of fish in turbid conditions.

Our study demonstrated that turbidity conditions (54 to 353 NTU) did not disturb the feeding success of juvenile winter flounder considering the high percentage ($92\% \pm 9.7$) of feeding fish and the percentage of the digestive tract area filled with food. Juveniles also seemed to feed equally well in turbid or in clear conditions. However, the turbidity significantly influenced the IOD index: a higher IOD index was observed in clear water (0 to 54 NTU) than in turbid conditions (54 to 353 NTU). The IOD index takes into account the filled area of the digestive system and the intensity of colouration. In fact, the intensity



of colouration varies as a function of the quantity of *Artemia* nauplii prey ingested: a pale colouration indicates an empty stomach or one with few prey while a dark colouration indicates a stomach that is full or contains a larger number of prey. This index is a good indicator of the volume of food in the digestive tract due to a more precise evaluation of stomach fullness. Studies have demonstrated that estuarine pelagic fish, especially larval and juvenile forms, may actively seek out turbid waters in the natural field (Bruton, 1979; Blaber and Blaber, 1980; Cyrus and Blaber, 1987a). Gradall and Swenson (1982) provided evidence of an active preference of turbid over clear conditions in juvenile brook trout (*Salvelinus fontinalis*) and creek chub (*Semotilus atromaculatus*), whereas Cyrus and Blaber (1987b) showed the preference of *Monodactylus argenteus* to intermediate turbidity (10-80 NTU). In contrast, *Rhabdosargus holubi*, *Acanthopagrus berda*, *Pomadasys commersonni*, and *Terapon jarbua* were not disturbed by turbidity levels higher than 80 NTU (Cyrus and Blaber, 1987b). Nevertheless, differences among study conclusions may simply result from the levels of turbidity, species, life stages, and habitat examined.

Boehlert and Morgan (1985) observed a higher feeding rate in Pacific herring larvae (*Clupea pallasii*) in turbid conditions than in clear water conditions. This increase was explained by an enhancement of the visual contrast between a predator and its prey. Larvae responded faster to the presence of prey against a turbid background than in clear water conditions. We may presume that contrast enhancement, induced by turbidity, could enable juvenile winter flounder to detect brine shrimp nauplii prey more quickly. Moreover, brine shrimp, which are relatively slow-moving prey, may not be able to escape rapidly from the limited field of vision of the juvenile winter flounder. Juveniles could then

appear to have an advantage in turbid conditions compared to clear water conditions. However, in our experimental set-up, brine shrimp nauplii moved rapidly due to the airlift system that maintained the sediments in suspension. Thus it may be that feeding success in our experiment was not influenced by the reduced swimming capacity of brine shrimp nauplii. Moreover, Tanaka et al. (1989) reported that juvenile Japanese flounder migrated up in the water column if prey were less abundant on the sea bottom. In the previous study, juveniles were located in light conditions that were optimal for feeding. We may assume that juveniles can then change their feeding behaviour to compensate for a reduced visual field and move into the better-illuminated surface layers to feed more efficiently. In our present study, the probability of prey detection by juvenile winter flounder resulting from the volume searched or the reaction distance was not impaired by turbidity, considering the high percentage of feeding fish. Nevertheless, some studies on turbidity effects also show the influence of prey assemblages that may vary in density, species composition, motility, and size distribution.

Gardner (1981) observed that turbidity did not have a significant effect on the size selectivity patterns exhibited by bluegills. However, turbidity may then alter taxon selectivity by planktivorous fish, causing fish to capture only more slowly moving prey types. Moreover, the reaction distance can be modified due to the density of prey introduced during the experiment. In fact, a high prey density decreases the search time for fish and consequently increases the encounter rate and the feeding success. We may also presume that the prey density used during our experiment did not influence the feeding behaviour of juvenile winter flounder. To our knowledge, no studies have been conducted

on the reaction distance in juvenile flatfishes. However, it has been previously noted that turbidity in pelagic fish could negatively modify the encounter rate and reaction distance between a predator and its prey (Vinyard and O'Brien, 1976; Barrett et al., 1992). The contrast degradation theory predicts that the visibility of objects that can be seen at a large distance in clear water will be disproportionately reduced in turbid water compared to that of objects that are visible at a shorter distance in clear water (De Robertis et al., 2003). Contrast degradation has an effect similar to fog, which can greatly diminish long-range visibility without having a large short-range effect (Lythgoe, 1979; De Robertis et al., 2003). Miner and Stein (1993) noted that the reaction distance of bluegill larvae declined with an increasing level of turbidity (Howick and O'Brien, 1983; O'Brien, 1987). Studies on pelagic fish have also suggested that the probability of prey detection was proportional to the reaction distance (Confer and Blades, 1975; Hairston et al., 1982). The search volume or reaction distance of juvenile winter flounder could be expected to decrease with increasing turbidity. However, a reduced reaction distance may not result in reduced feeding ability. In fact, when reaction distance is short, there are fewer suspended particles between predator and prey to reflect light and interfere with detection. De Robertis et al. (2003) demonstrated that high turbidity significantly decreased prey consumption by chum salmon (*Oncorhynchus keta*) and walleye pollock (*Theragra chalcogramma*), two planktivores, at a higher illumination level but not at a lower one. Prey will be more visible at a shorter distance in a lower illumination level, and this will reduce the effects of contrast degradation. In addition, Gregory and Levings (1996) demonstrated that encounter rate or reaction distance during turbidity treatments may not be sufficiently limiting to cause a reduction in capture rates due to experimental container size.

Flatfish adaptation is principally the ability of juveniles or adults to bury themselves in sediments and their faculty to mimic sediment colour and appearance (Pearcy, 1962). Nevertheless, earlier in their life cycle, i.e., at the end of metamorphosis, the newly settled winter flounder are translucent, due to a lack of pigmentation, and are also more likely to be detected by predators. The risk of predation on juvenile winter flounder should be lower in turbid than in clear water, with the visual contrast of translucent juvenile winter flounder enhanced by a full digestive tract. In the laboratory, when juveniles were maintained on the clay substratum, we could easily distinguish the feeding fish by the stomach colouration. Juveniles could then have a higher potential risk of predation and may act and feed accordingly. Several studies have suggested that some pelagic fish species may use turbidity as a cover against predators (for reviews: Miller, 1979; Bruton, 1985, Gregory, 1991; Gregory and Northcote, 1993). Gregory (1993) showed that juvenile chinook may also reduce their predator avoidance behaviour in turbid conditions. Moreover, Vandenbyllaardt et al. (1991) suggested that differential retinal development between piscivorous walleye and their minnow prey makes foraging in turbid conditions more successful for predators.

Our study demonstrated equally that juvenile size did not modify the feeding success of juvenile winter flounder neither the percentage of the digestive tract area filled with *Artemia*. We have tested the influence of juvenile size in clear water conditions to eliminate the potential risk of a turbidity effect.

In summary, results from our study indicate that turbidity did not induce significant reductions in the percentage of feeding juvenile winter flounder and in the percentage of the area of the digestive system containing food. Nevertheless, the IOD index was higher in clear conditions compared to turbid conditions. These results support the hypothesis that turbidity can be viewed as an advantage for juvenile flounder due to the decrease of predation pressure on them and to a decrease in their reaction distance, which allows better prey detection.

CONCLUSION GÉNÉRALE

Dans le but de répondre à l'objectif de notre étude, nous avons déterminé l'effet de la turbidité sur le pourcentage de juvéniles de plie rouge s'alimentant, sur le pourcentage de remplissage des estomacs, ainsi que sur l'indice IOD (aire d'alimentation x intensité de coloration). Notre étude indique que la turbidité n'a que peu d'effet sur le succès d'alimentation des juvéniles de plie rouge (*Pseudopleuronectes americanus*). La turbidité n'a pas eu d'effet significatif sur la proportion de juvéniles s'alimentant, ni sur le degré de remplissage des estomacs. En revanche, l'indice IOD des juvéniles est significativement plus élevé en absence qu'en présence de turbidité. La turbidité pourrait ainsi agir sur le nombre de proies ingérées. Toutefois, l'indice IOD ne semble pas être modifié par les niveaux croissants de turbidité. Les résultats démontrent donc que la turbidité n'influencerait que dans un mode bimodal (absence-présence) la capacité des juvéniles à capturer les proies vivantes présentes dans le milieu.

Cette étude semble donc très importante dans le cadre d'une éventuelle gestion de l'habitat naturel de poissons nectobenthiques.

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