J. Appl. Ichthyol. 23 (2007), 240–245

ISSN 0175–8659

Received: July 22, 2006
Accepted: November 7, 2006
doi: 10.1111/j.1439-0426.2007.00852.x

Effect of temperature and salinity on the gastric evacuation of juvenile sole *Solea solea* and *Solea senegalensis*

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Summary

The juveniles of Senegal sole, *Solea senegalensis*, Kaup 1858, and common sole, *Solea solea* (Linnaeus 1758) concentrate in estuarine and coastal nurseries of widely differing temperatures and salinities. Yet, little is known about the effect of these physiologically important variables on the gastric evacuation rates of these species. Gastric evacuation experiments were performed on juveniles of *S. senegalensis* and *S. solea*. Three temperatures were tested, 26, 20 and 14°C at a salinity of 35‰. A low salinity experiment was also carried out at 15‰, at 26°C. Experimental conditions intended to reflect conditions in estuarine and coastal nurseries where juveniles of these species spend their first years of life. The relation between stomach contents and time was best described by exponential regression models for both species. An analysis of covariance (ANCOVA) was performed in order to test differences in evacuation rate due to temperature and salinity (slope of evacuation time against stomach contents) for each species. While increasing temperature increased evacuation rates in both species (although not at 26°C in *S. solea*), the effect of low salinity differed among species, leading to a decrease in gastric evacuation rate in that of *S. senegalensis* and an increase in *S. solea*. Differences in gastric evacuation rate between species were related to its metabolic optimums and to its distribution in the nursery area where fish were captured. Implications for the habitat use of estuarine and coastal nurseries are discussed.

Introduction

The evaluation of feeding interactions between species and quantification of predation requires food consumption estimates. A common approach to estimating food consumption in the wild is the combination of field data on stomach contents and information on gastric evacuation rates (e.g. Bajkov, 1935; Bromley, 1994). Food consumption models generally assume that over long time periods the rate at which food is evacuated from the stomach is equal to the rate at which food is ingested.

The determination of gastric evacuation rates in commercial fish species is also important for aquaculture purposes. Much of the fish cultured in Portugal and Spain comes from semi-extensive multi-species fish-farms, where estimation of food consumption by each species is crucial for management purposes.

This study focuses on 0-group juveniles of Senegal sole *Solea senegalensis*, Kaup 1858, and common sole, *Solea solea*, (Linnaeus 1758). These are benthic flatfishes with sympatric distribution from the Bay of Biscay to Senegal and the western Mediterranean (Quero et al., 1986). They are very similar morphologically as well as in ecological needs. Both species are important predators and therefore can be of great importance to the dynamics and composition of the biological communities in the estuarine and coastal systems where they occur. Both types of sole have high commercial value. *S. senegalensis* is a species of increasing interest in aquaculture and is commonly cultured in the Portuguese and Spanish southern coasts (Dinis et al., 1999; Imsland et al., 2003).

The first year of life is a key stage in fish development, particularly for species like the sole that concentrate in large densities in estuarine and coastal nurseries where space and food partitioning become an issue (e.g. Schoener, 1974; Ross, 1986). In these nurseries, fish juveniles benefit from the reduced number of predators and conditions favourable to rapid growth, such as high temperatures and prey abundance. However, they must withstand temperature and salinity amplitudes much broader than those found in the sea (Haedrich, 1983). Therefore, the estimation of food consumption in estuarine and coastal waters must take into account the influence of temperature and salinity in the gastric evacuation of fish.

Temperature is probably the most studied variable influencing digestion and gastric evacuation (Bromley, 1994). Although there are some exceptions, most studies found an exponential relationship between the temperature and gastric evacuation rate (e.g. Elliot and Person, 1978; Elliott, 1992; Bromley, 1994).

Salinity is not usually addressed in gastric evacuation studies, yet there is evidence that this factor should be taken into account when dealing with euryhaline fish. It is well known that teleost fish hypo-osmoregulate in marine environments, and are therefore faced with osmotic water loss and the passive gain of many ions (Smith, 1930; Evans, 1993). To avoid dehydration they constantly drink ambient water, absorbing the majority of the imbibed volume within the intestine. Euryhaline fish when faced with low salinities will lower their drinking rate and eventually stop drinking (Smith, 1930; Evans, 1993). The drinking rate has an important influence on gastric evacuation because every time fish drink, part of the stomach content will be flushed into the intestine. Osmoregulation is also known to affect food intake (e.g. Buckley et al., 1995; Peterson-Curtis, 1997; Imsland et al., 2001), food conversion efficiency (Lambert et al., 1994; Likongwe et al., 1996; Alava, 1998; Imsland et al., 2001), hormone balance (McCormick, 1996; Bjornsson et al., 1998) and the metabolic rate (Woo and Kelly, 1995; Swanson, 1996; Dutil et al., 1997).

The present study aims to: (i) investigate effects of temperature and salinity in the gastric evacuation of *S. solea* and

S. senegalensis juveniles fed discrete meals of *Nereis diversicolor* (Müller, 1776), to (ii) relate it to the estuarine environment where they spend their early life and to (iii) compare estuarine and coastal nurseries' habitat use constrains for juvenile sole.

Materials and methods

Study area

The Tagus estuary, where the fish used in the experiments were captured, is one of the largest estuaries in Western Europe (325 km^2). It is a partially mixed estuary with a tidal range of *ca.* 4 m. Approximately 40% of the estuarine area is intertidal. In previous studies two important sole nurseries were identified in the Tagus estuary (Vila Franca de Xira, and Alcochete) by Costa and Bruxelas (1989) and Cabral and Costa (1999). The uppermost area, Vila Franca de Xira, is deeper (mean depth 4.4 m), presents a lower and highly variable salinity and has a higher proportion of fine sand in the substrate (approximately 40%). The Alcochete nursery is shallower (mean depth 1.9 m), and more saline, with lower variability in salinity, and the substrate is mainly composed of mud (mean value 60.4%) (Cabral, 1998; Cabral and Costa, 1999). In the uppermost nursery, Vila Franca de Xira, both species are present; highest densities of *S. solea* occur at the lowest salinity area, closest to the freshwater input, whiile *S. senegalensis* presents high densities over a wider salinity range within the nursery (Cabral and Costa, 1999). At the Alcochete nursery only *S. senegalensis* is present (Cabral and Costa, 1999).

Gastric evacuation experiments

S. senegalensis and *S. solea* were captured in the Tagus estuary and selected according to their size. Prior to experiments fish were held in circular tanks with capacities of 350 L for a minimum of 4 weeks (maximum stocking density 120 fish per 350 L). Fish were then transferred to 160 L aquaria equipped with mechanical and biological filter units. Temperature was regulated with a precision of ± 0.1°C. Salinity was regulated with a precision of 0.1‰. Temperature and salinity were monitored daily. Fish were exposed to a day length of 12 h.

For the gastric evacuation experiments fish were transferred into compartments to allow controlled feeding of each individual. Compartments measured $25 \times 30 \times 40$ cm (length, width, depth). Experimental fish were 0-group, weighted between 3.00 and 5.00 g (mean = 4.42; SD = 0.60) and measured between 70 and 85 mm (total length) (mean = 75.48; SD = 4.55). Fish were kept for 3 weeks in these compartments prior to the gastric evacuation experiments. During this period they were fed with the same prey given during the experiment.

A preliminary experiment was carried out in order to determine the period of complete stomach and digestive tube emptying and assess the appropriate interval between observations. In the preliminary experiment observations were made 30 min after feeding and every hour for 48 h.

Prior to the evacuation experiments fish were not fed for 24 h to allow a complete emptying of the stomachs. The experimental meal was offered to the fish for 15 min, as in the 3-week feeding period. After feeding, fish were anaesthetized in 1 : 3000 solution of tricaine methanesulphonate (MS 222 Sandoz) and sacrificed with a cut on the anterior spine.

Observations were made at 0, 2, 3, 4, 8, 14, 16 and 20 h after feeding (eight fish were used at each experimental time). Fish were measured (total length with 1 mm precision) and weighed (wet weight with 0.01 g precision). Stomach contents were weighed (wet weight with a 0.001 g precision).

Ragworm, *N. diversicolor*, a natural prey of *S. senegalensis* and *S. solea* (Cabral, 2000a), was reared in laboratory aquaria. Immediately before the experiment, worms were weighed (wet weight with a 0.001 g precision) and those weighing 0.300 g were selected, according to experimental needs. Prey weight was determined from previous experience of stomach contents analysis of specimens captured in the Tagus estuary.

This experiment intended to mimic temperatures these species find during the first year of life in nursery areas where both are sympatric. Three water temperatures were tested: 26°C, commonly found in estuarine nursery areas during summer; 20°C, common in spring and autumn; and 14°C, common during winter (Cabral, 2000a). Since the period of most intense growth of these species occurs during summer (Cabral, 2003), 26°C was the temperature chosen for the salinity experiment. During the 4-week period fish spent in circular tanks the temperature was gradually altered, starting with the temperature measured on the estuarine waters where they were caught and until the experimental temperature was reached. Temperature was altered at a rate of no more than 2°C per week. Being estuarine species they endure higher temperature changes in one day due to tides in their natural environment. Changes of 6°C over a time of 4 weeks reflect changes in the natural environment, as similar changes happen in the Tagus estuary around June–July (from 20 to 26°C), around September–October (from 26 to 20°C), around November–December (from 20 to 14°C) and around April–May (from 14 to 20°C).

The salinity experiment intended to compare gastric evacuation in coastal and estuarine nurseries and was therefore conducted at 35‰, a typical salinity in coastal waters, and at 15‰, a common salinity in the Tagus estuary nursery areas as well as in other estuarine nurseries where these species occur. During the 4-week period that fish spent in circular tanks the salinity was gradually altered, beginning with the salinity measured on the estuarine waters where they were caught until the experimental salinity was reached. Salinity was altered at a rate of no more than 5‰ per week.

Data analysis

Mean and standard deviation values were calculated for each set of replicates in order to determine time of total stomach emptying. A regression procedure was conducted in each of the datasets and it was concluded that the relation between stomach content and time was exponential. Since the exact time in which stomachs became empty cannot be determined, experiments in which empty stomachs occurred were excluded from the regression analysis to avoid bias (Bromley, 1994; Temming and Andersen, 1994). Stomachs were considered empty when the weight of their contents was less than 1% of the initial meal weight.

An analysis of covariance (ANCOVA) was conducted with the software STATISTICA to test differences in the evacuation rate due to temperature and salinity (slope of evacuation time against stomach contents) for each species. In order to fulfill the requirements of this analysis the data on stomach contents was log transformed. A significance level of 0.05 was considered.

Results

Total stomach emptying time decreased with increasing temperature in *S. senegalensis*, as a result of the observed

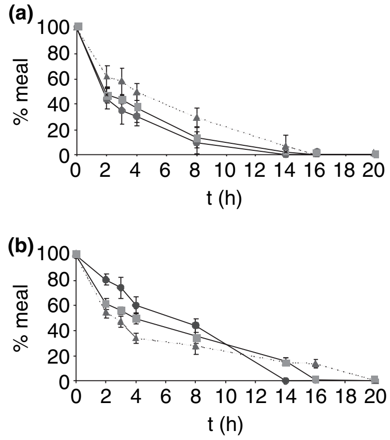

Fig. 1. Mean percentage of meal in stomachs of *S. senegalensis* (a) and *S. solea* (b) (bars indicate standard deviation values; n = 8) according to experiment time at 26°C (●), 20°C (■) and 14°C (▲)

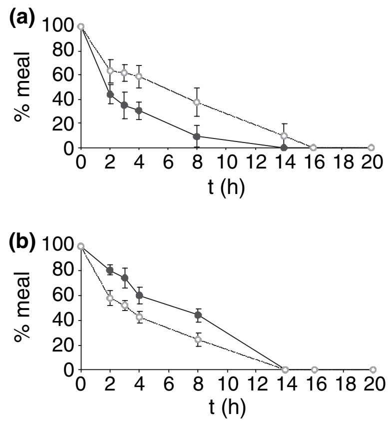

Fig. 2. Mean percentage of meal in stomachs of *S. senegalensis* (a) and *S. solea* (b) (bars indicate standard deviation values; n = 8) according to experiment time at a salinity of 35‰ (●) and 15‰ (○)

increase in gastric evacuation rate with temperature (P < 0.05). The lower evacuation rate observed at a lower salinity (15‰) (P < 0.05), when compared to seawater salinities (35‰), resulted in an increase of total stomach emptying time.

The period for total stomach emptying for *S. senegalensis* was 14 h for fish held at 26°C and 16 h for fish held at 20 and 14°C (Fig. 1). The period for total stomach emptying for individuals held at 15‰ (at 26°C) was 16 h (Fig. 2). The relation between stomach contents and time was best described by an exponential regression.

Gastric evacuation rate at 26°C was 0.325 g h^{-1}, at 20°C was 0.259 g h^{-1} and at 14°C was 0.152 g h^{-1} (Fig. 3). Gastric evacuation rate at 15‰ was 0.118 g h^{-1} (Fig. 4), considerably lower than at 35‰ (Fig. 4).

Total stomach emptying time decreased with increasing temperature in *S. solea*. Gastric evacuation rate increased with increasing temperature from 14 to 20°C, yet at 26°C a decline was observed (P < 0.05). Contrary to the observation in *S. senegalensis*, the evacuation rate in *S. solea* was higher at the lower salinity (15‰) (P < 0.05) when compared to the seawater salinity (35‰), however the time for total stomach emptying was the same.

The period for total stomach emptying for *S. solea* was 14 h for fish held at 26°C, 16 h at 20°C and 20 h at 14°C (Fig. 1). The period for total stomach emptying for individuals held at 15‰ (at 26°C) was 14 h (Fig. 2). The relationship between stomach contents and time was also best described as an exponential regression. Gastric evacuation rate at 26°C was 0.104 g h^{-1}, at 20°C was 0.124 g h^{-1} and at 14°C was 0.113 g h^{-1} (Fig. 3). Gastric evacuation rate at 15‰ (26°C) was 0.174 g h^{-1}, considerably higher than at 35‰ (Fig. 4).

Discussion

Both temperature and salinity have an important effect on gastric evacuation in *S. solea* and *S. senegalensis* and should be addressed when estimating food consumption in natural and semi-natural systems. While increasing temperature increased

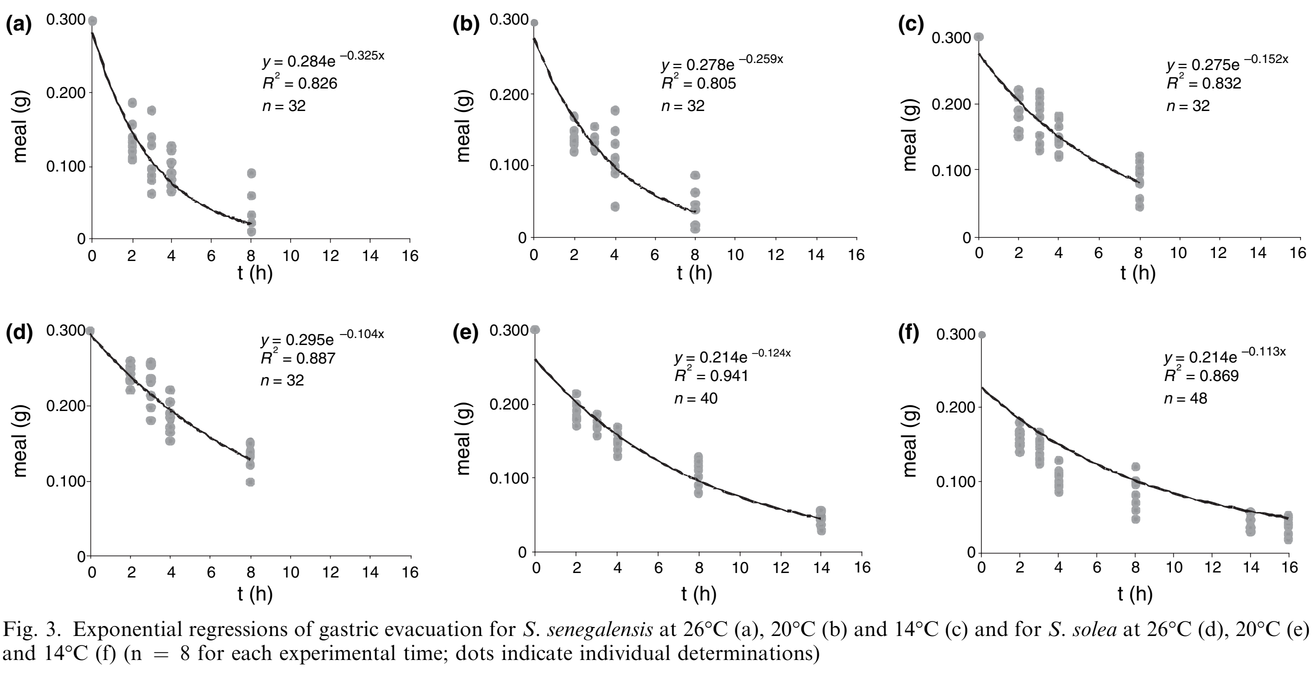

Fig. 3. Exponential regressions of gastric evacuation for *S. senegalensis* at 26°C (a), 20°C (b) and 14°C (c) and for *S. solea* at 26°C (d), 20°C (e) and 14°C (f) (n = 8 for each experimental time; dots indicate individual determinations)

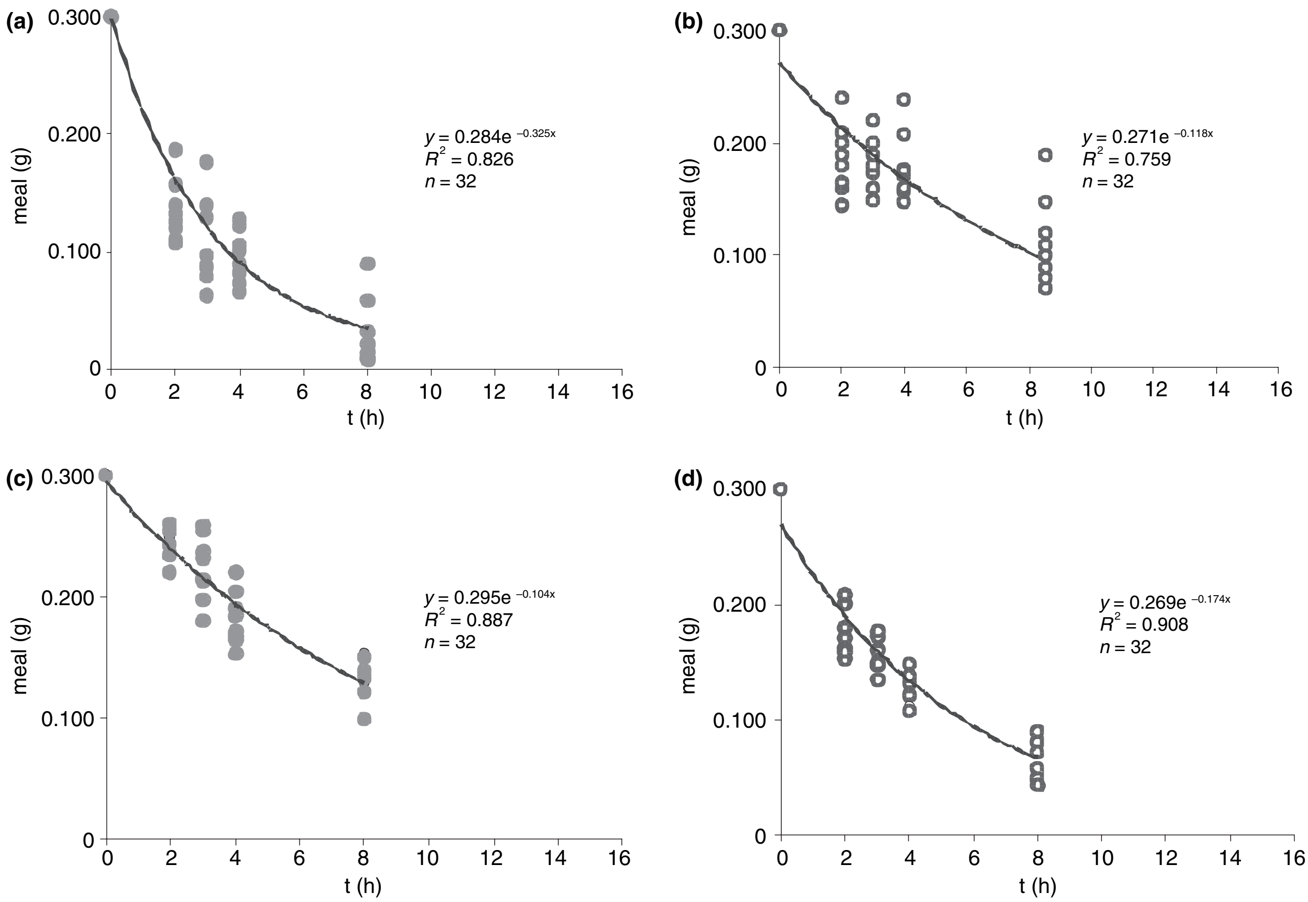

Fig. 4. Exponential regressions of gastric evacuation for *S. senegalensis* at salinity 35‰ (a) and 15‰ (b) and for *S. solea* at 35‰ (c) and 15‰ (d) (n = 8 for each experimental time; dots indicate individual determinations)

evacuation rates in both species (although not at 26°C in *S. solea*), the effect of low salinity differed between species, leading to an increase in gastric evacuation rate in *S. solea* and a decrease in *S. senegalensis*.

Several studies have focused on the effect of temperature over gastric evacuation in several fish species (e.g. Elliot, 1972; Elliot and Person, 1978; Elliott, 1992; Bromley, 1994) including flatfish (e.g Jobling et al., 1977; Flowerdew and Grove, 1979; Jobling, 1980; Hurst, 2004). The works of Kruuk (1963) and De Groot (1971) showed that evacuation rates of *S. solea* increase with increasing temperature. The effect of temperature on gastric evacuation is a well known phenomenon that enables fish to have higher daily food consumption rates at higher temperatures.

Factors that affect gastric evacuation may also affect appetite and food intake. A correlation between gastric emptiness and food intake was found for salmonids (Brett, 1971; Elliot, 1975a,b), *Gasterosteus aculeatus* (Linnaeus 1758) (Tugendhat, 1960; Beukema, 1968) and *Euthynnus pelamis* (Linnaeus 1758) (Magnuson, 1969). It is thought that appetite is mediated by stretch receptors in the stomach wall similar to those of higher animals (Stevenson, 1969). It is also well known that when food is unlimited, ingestion increases with increasing temperature, reaching a peak at the optimum temperature before declining steeply as the temperature approaches the species thermal limit (Jobling, 1993; Yamashita et al., 2001). The same should happen for gastric evacuation since these processes are strongly related. As *S. senegalensis* is a subtropical species the highest temperature tested, 26°C, is probably well below its thermal upper limit, which is reflected by the steadily increasing evacuation rates with temperature. *S. solea*, however, is a temperate species with a metabolic optimum temperature of approximately 19°C (LeFrançois and Claireaux, 2003). Thus, the observed decline in *S. solea* evacuation rate at 26°C is quite probably due to thermal stress. In estuarine nurseries such as the Tagus estuary where these sole are sympatric, *S. solea* is at a disadvantage during the summer months when juveniles of both species concentrate in shallow waters that are rich in prey but where temperatures warm up well above the *S. solea* metabolic optimum.

Salinity is usually not addressed in gastric evacuation studies, since most of the work on gastric evacuation has been aimed at incorporating food consumption of adult fish stocks in multi-species models for fisheries management, such as the North Sea multi-species model (Gislason and Helgason, 1985; Pope, 1991). However, in order to study food consumption of juvenile marine fish that spend their first two years in estuarine nurseries, salinity must be taken into account, since it is the single most important factor determining teleost fish drinking rates (Smith, 1930; Evans, 1993). Antibiotic evacuation studies reported stomach content leakage in marine fish held at 35‰ due to permanent drinking (Guichard, 2000). This does not happen in freshwater fish since they do not drink (Smith, 1930; Evans, 1993). Euryhaline fish such as the sole held at low salinities will lower their drinking rate and therefore present higher retention of stomach contents and lower evacuation rates.

Furthermore, several studies show that although feeding rates increase with salinity, the food conversion efficiency decreases (Saillant et al., 2003; Wuenschel et al., 2004), possibly due to higher metabolic costs at seawater salinity. This means that fish at lower salinities operate at higher efficiency, being able to maintain high growth rates at lower ration levels. This has important implications when assessing habitat use constrains, in that estuarine nurseries will provide conditions that allow higher food conversion than the coastal nurseries.

Interestingly, low salinity had a different effect according to the sole species studied. *S. solea* seems to be better adapted to low salinities, which is reflected in its higher evacuation rates at 15‰ than at seawater; the opposite was observed in *S. senegalensis*. *S. solea* and *S. senegalensis* are very similar and are considered sister species, yet when in sympatry the *S. solea* seems to prefer lower salinity habitats than *S. senegalensis*, as has been observed in the Tagus estuary (Cabral and Costa, 1999; Cabral et al., in press) as well as in other estuaries (Dorel et al., 1991; Marchand, 1993; Cabral, 2000b; Cabral et al., in press). A different level of adaptation to low salinity, as evacuation rates seem to indicate, is probably the most important factor determining these species partition of space within the nursery area.

Other authors have observed species specific use of nursery habitats concerning salinity for other flatfish species such as southern flounder and summer flounder in North America (Powell and Schwartz, 1977; Burke et al., 1991), among the flatfish community in North Carolina (North America) (Walsh et al., 1999), for Japanese flounder in Japan (Yamashita et al., 2001), among the flatfish community of the Sado estuary (Portugal) (Cabral, 2000b), and in the flatfish community of the Ems estuary (the Netherlands) (Jager et al., 1993).

Although many factors other than temperature and salinity are important for the evaluation of habitat quality, our results indicate that estuarine nurseries provide salinity conditions more favourable than coastal nurseries for *S. solea*, since this species has higher evacuation rates at low salinities, yet in many estuarine systems it will endure summer temperatures that lead to thermal stress, which would not happen at the coast. For *S. senegalensis*, estuarine nurseries provide favourable temperatures during the nursery period. The decrease in gastric evacuation rate at low salinities is probably compensated by higher food conversion, as is observed in other euryhaline species (Saillant et al., 2003; Wuenschel et al., 2004).

One important factor that may influence food uptake in fish nurseries is predator pressure. Predation is now recognized as one of the main factors influencing prey behaviour (review in Lima, 1990) and predator avoidance is known to lead to changes in habitat use, feeding, morphology and growth of prey (Jones and Paszkowski, 1997; Turner et al., 1999). Maia et al. (in press) reported that predator presence led to a 10% decrease in foraging activity of *S. senegalensis*, meaning that nurseries that provide appropriate temperature and salinity levels may have its habitat quality potential hampered by high densities of juvenile fish predators.

The present work provides important information upon which food consumption models can be estimated for *S. senegalensis* and *S. solea*. Further experimental research using broader temperature and salinity ranges will bring new insight into the effect of these important factors over these species dynamics. Studies on the effects of other factors such as fish size and prey type will allow for a more comprehensive outlook on the gastric evacuation process in sole as well as the production of generalized models of gastric evacuation, such as those already available for other species (e.g. Jobling, 1980; dos Santos and Jobling, 1991; Koed, 2001; Temming et al., 2002; Hurst, 2004; Andersen and Beyer, 2005).

Acknowledgements

The authors would like to thank everyone who was involved in the aquarium maintenance, and Dr Ana Passos for providing the ragworms. This study was co-funded by the European Union through the FEDER-Fisheries Programme (MARE), as well as the Fundação para a Ciência e a Tecnologia (FCT) which financed several of the research projects related to this work. The authors would also like to thank the two anonymous referees whose comments contributed to the improvement of the earlier version of the manuscript.

References

Alava, V. R., 1998: Effect of salinity, dietary lipid source and level on growth of milkfish (*Chanos chanos*) fry. Aquaculture **167,** 229–236.

Andersen, N. G.; Beyer, J. E., 2005: Gastric evacuation of mixed stomach contents in predatory gadoids: an expanded application of the square root model to estimate food rations. J. Fish Biol. **67,** 1413–1433.

Bajkov, A. D., 1935: How to estimate the daily food consumption of fish under natural conditions. Trans. Am. Fish Soc. **65,** 288–289.

Beukema, J. J., 1968: Predation by the 3-spined stickleback (*Gasterosteus aculeatus*): the influence of hunger and experience. Behaviour **31,** 1–126.

Bjornsson, B. T.; Stefansson, G. V.; Berge, A. I.; Hansen, T.; Stefansson, S. O., 1998: Circulating growth hormone levels in Atlantic salmon smolts following seawater transfer: effects of photoperiod regime, salinity, duration of exposure and season. Aquaculture **168,** 121–137.

Brett, J. R., 1971: Satiation time, appetite and maximum food intake of sockeye salmon (*Onkorhynchus nerka*). J. Fish Res. Board Can. **28,** 409–415.

Bromley, P. J., 1994: The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. Rev. Fish Biol. Fish. **4,** 36–66.

Buckley, J. A.; Steinberg, N. D.; Conover, D. O., 1995: Effects of temperature, salinity and fish size on growth and consumption of juvenile bluefish. J. Fish Biol. **47,** 696–706.

Burke, J. S.; Miller, J. M.; Hess, D. E., 1991: Immigration and settlement pattern of *Paralichthys dentatus* and *P. lethostigma* in a estuarine nursery ground, North Carolina, USA. Neth. J. Sea Res. **27,** 393–405.

Cabral, H.N., 1998: Utilização do estuário do Tejo Como area de viveiro pelos linguados *Solea solea* (L. 1758) e *Solea senegalensis* Kaup, 1858, e robalo. *Dicentrarchus labrax* (L. 1758) PhD thesis, University of Lisbon, Lisbon.

Cabral, H. N., 2000a: Comparative feeding ecology of sympatric *Solea solea* and *Solea senegalensis*, within the nursery areas of the Tagus estuary, Portugal. J. Fish Biol. **57,** 1550–1562.

Cabral, H. N., 2000b: Distribution and abundance patterns of flatfishes in the Sado estuary, Portugal. Estuaries **23,** 351–358.

Cabral, H. N., 2003: Differences in growth rates of juvenile *Solea solea* and *Solea senegalensis* in the Tagus estuary, Portugal. J. Mar. Biol. Ass. UK **83,** 861–868.

Cabral, H. N.; Costa, M. J., 1999: Differential use of nursery areas within the Tagus estuary by sympatric soles, *Solea solea* and *Solea senegalensis*. Environ. Biol. Fishes **56,** 389–397.

Cabral, H. N.; Vasconcelos, R.; Vinagre, C.; França, S.; Fonseca, V.; Maia, A.; Reis-Santos, P.; Lopes, M.; Ruano, M.; Campos, J.; Freitas, V.; Costa, M. J., Relative importance of estuarine flatfish nurseries along the Portuguese coast. J. Sea Res. (in press).

Costa, M. J.; Bruxelas, A., 1989: The structure of fish communities in the Tagus estuary, Portugal, and its role as a nursery for commercial species. Sci. Mar. **53,** 561–566.

De Groot, S. J., 1971: On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). Neth. J. Sea Res. **5,** 121–196.

Dinis, M. T.; Ribeiro, L.; Soares, F.; Sarasquete, C.; Stickney, R. R.; McVey, J. P., 1999: A review of the cultivation potential of *Solea senegalensis* in Spain and in Portugal. Flatfish Cult **176,** 27–38.

Dorel, D.; Desaunay, Y., 1991: Comparison of three *Solea solea* (L.) nursery grounds of the Bay of Biscay: distribution, density and abundance of 0-group and 1-group. ICES CM, 1991/G75, 8pp.

Dorel, D.; Koutsikopoulos, C.; Desaunay, Y.; Marchand, J., 1991: Seasonal distribution of young sole (*Solea solea* L.) in the nursery ground of the Bay of Vilaine (northern Bay of Biscay). Neth. J. Sea Res. **27,** 297–306.

Dutil, J. D.; Lambert, Y.; Boucher, E., 1997: Does higher growth rate in Atlantic cod (*Gadus morhua*) at low salinity result from lower standard metabolic rate or increased protein digestibility? Can J. Fish Aqua. Sci. **54,** 99–103.

Elliot, J. M., 1972: Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshw. Biol. **1,** 1–18.

Elliot, J. M., 1975a: The growth of brown trout (*Salmo trutta* L.) fed on maximum rations. J. Anim. Ecol. **44,** 805–821.

Elliot, J. M., 1975b: The growth of brown trout (*Salmo trutta* L.) fed on reduced rations. J. Anim. Ecol. **44,** 823–842.

Elliot, J. M.; Person, L., 1978: The estimation of daily rates of food consumption for fish. Anim. Ecol. **47,** 977–993.

Elliott, J. M., 1992: Rates of gastric evacuation in piscivorous brown trout, *Salmo trutta* L. Freshw. Biol. **25,** 297–305.

Evans, D. H., 1993: Osmotic and ionic regulation. In: The physiology of fishes. D. H. Evans (Ed.). CRC press, New York, USA, pp. 315–341.

Flowerdew, M. W.; Grove, D. J., 1979: Some observations of the effects of body weight, temperature, meal size and quality on gastric evacuation emptying time in the turbot, *Scophthalmus maximus* (L.), using radiography. J. Fish Biol. **14,** 229–238.

Gislason, H.; Helgason, T., 1985: Species interaction in assessment of fish stocks with special application to the North Sea. Dana **5,** 1–44.

Guichard, B., 2000: Devenir d'un aliment médicamenteux dans le tractus digestif du turbot (*Psetta maxima*, L.1758), pour l'étude des rejects d'un antibactérien en pisciculture marine. PhD thesis. University of Nantes, Nantes, France.

Haedrich, R. L., 1983: Estuarine Fishes. In: Ecosystems of the world 26. Estuaries and enclosed seas. B. Ketchum (Ed.). Elsevier Scientific, Amsterdam, pp. 183–207.

Hurst, T. P., 2004: Temperature and state-dependence of feeding and gastric evacuation in juvenile Pacific halibut. J. Fish Biol. **65,** 157–169.

Imsland, A. K.; Foss, A.; Gunnarson, S.; Berntssen, M. H. G.; Gerald, R. F.; Bonga, S. W., 2001: The interaction of temperature and salinity on growth and food conversion in juvenile turbot (*Scophthalmus maximus*). Aquaculture **198,** 353–367.

Imsland, A. K.; Foss, A.; Conceição, L. E. C.; Dinis, M. T.; Delbare, D.; Schram, E.; Kamstra, A.; Rema, P.; White, P., 2003: A review of the culture potential of *Solea solea* and *Solea senegalensis*. Rev. Fish Biol. Fish. **13,** 379–407.

Jager, Z.; Kleef, H. L.; Tydeman, P., 1993: The distribution of 0-group flatfish in relation to abiotic factors on the tidal flats in the brackish Dollard (Ems estuary, Wadden Sea). J. Fish Biol. **43,** 31–43.

Jobling, M., 1980: Gastric evacuation in plaice, *Pleuronectes platessa* L.: effects of dietary energy level and food composition. J. Fish Biol. **17,** 187–196.

Jobling, M., 1993: Bioenergetics: feed intake and energy partitioning. In: Fish ecophysiology. J. C. Rankin and F. B. Jensen (Eds.). Chapman & Hall, London, UK, 309pp.

Jobling, M.; Gwyther, D.; Grove, D. J., 1977: Some effects of temperature, meal size and body weight on gastric evacuation time in the dab *Limanda limanda* (L). J. Fish Biol. **10,** 291–298.

Jones, H. M.; Paszkowski, C. A., 1997: Effects of exposure to predatory cues on territorial behaviour of male fathead minnows. Env. Biol. Fish **49,** 97–109.

Koed, A., 2001: The effects of meal size, body size and temperature on gastric evacuation in pikeperch. J. Fish Biol. **58,** 281–290.

Kruuk, H., 1963: Diurnal periodicity in the activity of the common sole, *Solea vulgaris* Quensel. Neth. J. Sea Res. **2,** 1–28.

Lambert, Y.; Dutil, J. -D.; Munro, J., 1994: Effects of intermediate and low salinity conditions on growth rate and food conversion of Atlantic cod (*Gadus morhua*). Can. J. Fish. Sci. **51,** 1569–1576.

LeFrançois, C.; Claireaux, G., 2003: Influence of ambient oxygenation and temperature on metabolic scope and scope for heart rate in the common sole, *Solea solea*. Mar. Ecol. Progr. Ser. **259,** 273–284.

Likongwe, J. S.; Stecko, T. D.; Stauffer, J. R.; Carline, R. F., 1996: Combined effects of water temperature and salinity on growth and feed utilization of juvenile Nile tilapia *Oreochromis niloticus* (Linneaus). Aquaculture **146,** 37–46.

Lima, S. L., 1990: Evolutionarily stable antipredator behavior in isolated foragers: on the consequences of successful escape. J. Theor. Biol. **143,** 77–89.

Magnuson, J. J., 1969: Digestion and food consumption by skipjack tuna. Trans. Am. Fish Soc. **98,** 379–392.

Maia, A.; Vinagre, C.; Cabral, H. N., (in press) Foraging behaviour of *Solea senegalensis* Kaup, 1858, in the presence of a potential predator, *Carcinus maenas* Linnaeus. 1758.

Marchand, J., 1993: The influence of seasonal salinity and turbidity maximum variations on the nursery function of the Loire estuary (France). Neth. J. Aquat. Ecol. **27,** 427–436.

McCormick, S. D., 1996: Effects of growth hormone and insulin-like growth factor I on salinity tolerance and gill Na^+, K^+-ATPase in Atlantic salmon (*Salmo salar*): interaction with cortisol. Gen. Comp. Endocrinol. **101,** 3–11.

Peterson-Curtis, T. L., 1997: Effects of salinity on survival, growth, metabolism and behavior in juvenile hogchockers, *Trinectes maculates* (Achiridae). Environ. Biol. Fishes **49,** 323–331.

Pope, J., 1991: The ICES multispecies assessment working group: evolution, insights, and future problems. ICES J. Mar. Sci. **193**:22–33.

Powell, A. B.; Schwartz, F. J., 1977: Distribution of paralichthid flounders (Bothidae: Paralichthys) in North Carolina estuaries. Chesapeake Sci **18,** 334–339.

Quero, J. C.; Dessoutter, M.; Lagardere, F., 1986: Soleidae. In: Fishes of the North-eastern Atlantic and Mediterranean. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (Eds). UNESCO, Paris, France, pp. 1308–1324.

Ross, S. T., 1986: Resource portioning in fish assemblages: a review of field studies. Copeia **19,** 352–388.

Saillant, E.; Fostier, A.; Haffray, P.; Menu, B.; Chatain, B., 2003: Saline preferendum for the European sea bass, *Dicentrarchus labrax*, larvae and juveniles: effect of salinity in early development and sex determination. J. Exp. Mar. Biol. Ecol. **287,** 103–117.

dos Santos, J.; Jobling, M., 1991: Factors affecting gastric evacuation in cod, *Gadus Morhua* L., fed single meals of natural prey. J. Fish Biol. **38,** 697–713.

Schoener, T. W., 1974: Resource partitioning in ecological communities. Science **185,** 27–39.

Smith, H. W., 1930: The absorption and excretion of water and salts by marine teleosts. Am. J. Physiol. **93,** 480.

Stevenson, J. A. F., 1969: Mechanisms in the control of food and water intake in neural regulation of food and water intake (Ed: P. J. Morgane). Ann. N.Y. Acad. Sci. **157,** 1069–1083.

Swanson, C., 1996: Early development of milkfish: effects of salinity on embryonic and larval metabolism, yolk absorption and growth. J. Fish Biol. **48,** 405–421.

Temming, A.; Andersen, N. G., 1994: Modelling gastric evacuation in cod. A model applicable to the estimation of the daily ration of cod in the field. ICES J. Mar. Sci. **51,** 429–438.

Temming, A.; Bohle, B.; Skagen, D. W.; Knudsen, F. R., 2002: Gastric evacuation in mackerel: the effects of meal size, prey type and temperature. J. Fish Biol. **61,** 50–70.

Tugendhat, B., 1960: The normal feeding behaviour of the three spined stickleback *Gasterosteus aculeatus*. Behaviour **15,** 284–318.

Turner, A. M.; Fetterolf, S. A.; Bernot, R. J., 1999: Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail. Oecologia **118,** 242–247.

Walsh, H. J.; Peters, D. S.; Cyrus, D. P., 1999: Habitat utilization by small flatfishes in a North Carolina estuary. Estuaries **22,** 803–813.

Woo, N. Y. S.; Kelly, S. P., 1995: Effects of salinity and nutritional status on growth and metabolism of *Sparus sarba* in a closed seawater system. Aquacultre **135,** 229–238.

Wuenschel, M. J.; Joguvich, A. R.; Hare, J. A., 2004: Effect of temperature and salinity on the energetics of juvenile gray snapper (*Lutjanus griseus*): implications for nursery habitat value. J. Exp. Mar. Biol. Ecol. **312,** 333–347.

Yamashita, Y.; Tanaka, M.; Miller, J. M., 2001: Ecophysiology of juvenile flatfish in nursery grounds. J. Sea Res. **45,** 205–218.

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