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Variability of stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) in two spider crab populations (*Maja brachydactyla*) in Western Europe

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Abstract:

The ontogenic variations of nitrogen and carbon stable isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$) were investigated in two spider crab (*Maja brachydactyla*) populations inhabiting in different biotopes of Western Europe. The Iroise Sea population is localized in Western Brittany and characterized by a seasonal migration occurring on a large bathymetric and habitat gradient while the Seine Bay population, in the Eastern English Channel, remains in a more homogeneous environment during its migration. In the Iroise Sea population, $\delta^{13}C$ values increased significantly both with body size and age, revealing a shift towards "benthic-component" prey with spider crab growth. On the contrary, neither body size nor ageing gave rise to a significant trophic level change (derived from the $\delta^{15}N$). In this *M. brachydactyla* population, the seasonal migrations from coastal waters in summer to offshore habitats in winter involved significant but slight differences in both $\delta^{13}C$ and $\delta^{15}N$. In the Seine Bay population, low variations for both carbon and nitrogen were recorded related to either sex or size or seasonal migration. Thus, the $\delta^{13}C$ and $\delta^{15}N$ variability in the spider crab depends on the availability and diversity of prey in its different living habitats, as well as on the morphological aptitudes of individuals to feed on prey (individual's size).

Keywords: Carbon and nitrogen stable isotopes; Feeding; Growth; Marine decapod crustaceans; Migration

1. Introduction

Largely distributed along the Northwest Atlantic coast, the spider crab *Maja brachydactyla* (Crustacea:Decapoda:Majidae) is a species of commercial importance for French fisheries. *Maja brachydactyla*'s life cycle is from 5 to 8 years, consisting of two main periods of growth and reproductive phases separated by a terminal moult. During the growth phase, juvenile spider crabs inhabit shallow areas (depth: <10m) (Le Foll 1993). The juvenile stage lasts approximately two years until a terminal moult, at which time sexual maturity is achieved and no further moulting occurs (Le Foll 1993, González-Gurriarán et al. 1995, Sampedro et al. 1999). The postpubertal adults then undertake an autumn/winter migration from coastal nursery areas to offshore sites (depth: 40-120 m) (De Kergariou 1971, Latrouite & Le Foll 1989). Mating occurs in winter in deep waters, and adult spider crabs come back to shallow waters (<20m) the following spring, where the females will spawn (De Kergariou 1971, Stevcic 1977, González-Gurriarán et al. 1993, Le Foll 1993). In both shallow and deep waters, spider crabs can live either on soft sediment or rocky bottoms.

The make up of *Maja brachydactyla*'s diet remains to be accurately described. Direct observations in the field (Carlisle 1957, De Kergariou 1974), laboratory experiments (Stevcic 1967, 1968, Brosnan 1981) and studies based on gut contents (Stevcic 1967, De Kergariou 1974, Brosnan 1981, Bernárdez et al. 2000) have suggested that the spider crab has an omnivorous diet based on the consumption of prey commonly found in their habitat. Moreover, few studies have focused on the influence of sex, body size and habitat on the diet composition of this species (De Kergariou 1974, Bernárdez et al. 2000).

The measurement of stable isotopes of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) has recently become a useful tool to trace trophic relationships (Michener & Schell 1994) and food webs (Newell et al. 1995). This method assumes that, during ingestion, there is enrichment in heavy isotopes (i.e., ^{13}C or ^{15}N) compared to the food, which is compensated by the preferential excretion of light isotopes (Peterson & Fry 1987, Olive et al. 2003). The isotopic composition of an animal's tissue therefore reflects that of its prey (Dufour & Gerdeaux 2001), and different authors have suggested for all consumers a mean trophic enrichment in isotopic stable ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of about 0-1‰ and 3-4‰, respectively (De Niro & Epstein 1978, 1981, Minagawa & Wada 1984, Peterson & Fry 1987).

The $\delta^{15}N$ ratio is often used as a predictor of the relative trophic level (Vander Zanden et al. 1997, Pinnegar et al. 2002, Post 2002), whereas $\delta^{13}C$ values can be useful in evaluating sources of primary production in marine systems: $\delta^{13}C$ values are typically higher in inshore-

benthic food webs than in plankton-based systems (Hobson et al. 1995, Dauby et al. 1998). Conversely to stomach content analysis or direct observations which reflect the diet composition of an animal at the moment, stable isotope measurements of carbon and nitrogen in an organism's tissue provide a time-integrating method depending of the tissues turnover rates (Hesslein et al. 1993). $\delta^{15}N$ and $\delta^{13}C$ provide an average estimate of an organism's preferred diet which is less subject to temporal bias than gut content analyses. When an animal modifies its feeding and ingests prey with different isotopic composition from the previous intake, its isotopic carbon and nitrogen signature changes progressively (Riera et al. 2000).

The aims of this study were to examine the variability of nitrogen and carbon isotopic compositions in two different spider crab populations, and to test the various parameters which could explain this variability: demographic parameters (sex, age and size) and environmental parameters (geographic area and biotope). The study was carried out on two geographic sampling areas, the Iroise Sea (Western Brittany), and the Seine Bay (Eastern English Channel).

2. Material and methods

2.1. Sampling strategy

The two spider crab populations, one from the Iroise Sea and the other from the Seine Bay (Fig 1) were sampled in 2003-2004. The Iroise Sea, located in Western Brittany, is an important area for spider crab production. Juveniles were collected by scuba diving on sandy bottoms from the Bertheaume Bay nursery (48°21'51 N; 4°39'00 W), a 5-10 meter deep area colonized by a seagrass (*Zostera marina*) bed. In summer adult spider crabs live near the shores on rocky areas; samples were taken by scuba divers at depths of 10-15 m at Corbin Rock (48°17'50 N; 4°37'53 W). During winter, adult specimens were captured by professional fishermen on rocky bottoms in deep waters around 60-80 meters, at approximately 15 nautical miles from the coast (48°04'04 N; 4°57'59 W). In the second sampling area, the Seine Bay, juvenile and adult spider crabs were collected by scuba divers in summer near the Antifer oil terminal on muddy sands 5-10 m depth, with few rocks (49°44'81 N; 00°07'03 E). In winter, professional fishermen captured adult specimens at about 10 nautical miles from shore in deep waters around 30-40 m., on heterogeneous coarse sediments (49°49'10 N; 00°04'03 W).

2.2. Sample preparation.

A total of 131 and 92 spider crabs respectively from the Iroise Sea and Seine Bay were analyzed for their stable isotopic composition. After collection, the crab's gender was determined as well as the total fresh weight (W in g) and the carapace length (CL in mm) measured from the interval between the frontal spines back to the posterior edge of the carapace. Following the method developed by Le Foll (1993), the spider crab age classes were estimated on the basis of the hardness of the carapace, the quality and the abundance of the epibionts covering the carapace, and the wear of the claws and the rostrum. This information allowed us to classify each individual into one of five cohorts: from 0 to 1 year old (0-1), and 1 to 2 years old (1-2) for the juvenile specimens; from 2 to 3 years old (2-3), 3 to 4 years old (3-4) and over 4 years old (4+) for the adults.

For each specimen, the muscle was carefully dissected from the inner body for stable isotope analysis. Yokoyama et al. (2005) have recommended the use of muscle for isotopic analysis in decapod crustaceans because it provides a better measure of diet-tissue fractionation than a whole-body analysis does. Moreover, they have shown that acid treatment on muscle samples is unnecessary, provided that no debris of exoskeletons or any other inorganic carbonates are included in the samples. All sample tissues were kept at –20°C until being freeze dried, and further ground to obtain a fine homogeneous powder. Their water content is estimated from the weight loss during freeze drying.

2.3. Isotopic analysis

1±0.2mg of each dried sample was weighed in clean tin capsules for stable isotopic analysis. The stable isotope ratios of carbon and nitrogen were determined at the Scottish Crop Institute (Dundee, Scotland), by CF-IRMS analysis using a Europa Scientific ANCA-NT 20-20 Stable Isotope Analyser together with an ANCA-NT Solid/Liquid Preparation Module. As the samples contained more than 10% nitrogen, the CF-IRMS was operated in dual isotope mode, allowing $\delta^{15}N$ and $\delta^{13}C$ to be measured in the same sample. Stable isotope ratios were expressed in conventional δ notation as parts per mil (‰) according to the following equation:

$$\delta X_{sample} = [\ (R_{sample} / R_{reference}) - 1\ ]*1000$$

where X is ^{13}C or ^{15}N and R is the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio. Reference is VPDB (cretaceous PeeDee Belemnite) for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$. The

analytical precisions were ±0.2‰ for both nitrogen and carbon, as estimated from standards analyzed together with the samples.

2.4. Statistical analysis

All data follow a normal distribution according to the Shapiro-Wilk test ($p<0.05$). First of all, a Student test was used to compare the actual differences in mean $\delta^{13}C$ and $\delta^{15}N$ between spider crabs from the Iroise Sea and the Seine Bay. Then data on body weight, carapace length, $\delta^{13}C$ and $\delta^{15}N$ were subjected to correlation analysis using Pearson's correlation coefficient. Additionally, $\delta^{13}C$ and $\delta^{15}N$ in spider crab muscles from each sampling area were analyzed using ANOVA. If significant differences were found, processing pairs were compared by Tukey's HSD test. Statistical analyses were performed using Statistica Software 6.0.

3. Results

3.1. Comparison of the two populations

While the means were close, the Student test ($p<0.05$) revealed significant differences for both $\delta^{13}C$ and $\delta^{15}N$ measured in the spider crab muscles (all age, sex and sampling localizations mixed) between the two sampling areas. Spider crabs from the Seine Bay exhibited enriched values for both $\delta^{13}C$ and $\delta^{15}N$ compared to specimens from the Iroise Sea (mean ± SE, $\delta^{13}C$ = -15.02 ± 0.69‰ and -16.34 ± 1‰; $\delta^{15}N$ = 12.78 ± 0.62‰ and 12.56 ± 0.63‰, respectively). Stable isotope results are presented in table 1. A Pearson correlation analysis showed a significant correlation between $\delta^{13}C$ and $\delta^{15}N$ in the two populations (Iroise Sea: $r = 0.54$ and $p < 0.01$; Seine Bay: $r = 0.25$ and $p< 0.05$).

3.2. Body size variability

For each population, data on body weight (W) and carapace length (CL) were compared to stable isotopic ratios. For specimens from the Iroise Sea, significant positive correlations were obtained for both $\delta^{13}C$ and $\delta^{15}N$ with carapace length (Pearson coefficient: $r = 0.62$ and $p < 0.01$ for $\delta^{13}C$; $r = 0.53$ and $p < 0.01$ for $\delta^{15}N$) and body weight (Pearson coefficient: $r = 0.68$ and $p < 0.01$ for $\delta^{13}C$; $r = 0.54$ and $p < 0.01$ for $\delta^{15}N$). The smaller individuals (CL = 50-70 mm) presented depleted carbon and nitrogen isotopic values compared to larger ones with CL > 170 mm ($\delta^{13}C$ = -17.58 ± 0.59 and -15.01 ± 0.41‰; $\delta^{15}N$ = 11.92 ± 0.54 and 13.4 ± 0.32‰, respectively) (Fig. 2). As regards spider crabs from the Seine Bay, $\delta^{15}N$ was significantly

correlated with the body weight and the carapace length (Pearson coefficient: $r = 0.34$, $p < 0.01$ and $r = 0.48$, $p < 0.01$, respectively), but no relation was observed with the stable isotopic ratio of carbon.

3.3. Sex and age effects on isotope ratios in spider crabs from coastal waters

A two-way factorial Model I ANOVA was performed on $\delta^{13}C$ and $\delta^{15}N$ data of spider crabs collected in shallow coastal waters (summer period), in order to study the influence of both sex and age (5 age classes were tested) (Table 2). In the Iroise Sea, both nitrogen and carbon isotope ratios were influenced by the spider crab age. In the Seine Bay population, only the $\delta^{15}N$ values were affected by this factor. No significant relation was identified between sex and $\delta^{13}C$, and sex and $\delta^{15}N$ either in the Iroise Sea population or in the Seine Bay population.

In the Iroise Sea, the youngest spider crabs (0-1 year old) exhibited significantly more depleted values than all the other age classes, excepting the 2-3 year old specimens, for both $\delta^{13}C$ and $\delta^{15}N$ (Tukey-Kramer test, $p<0.01$) (Fig. 3). The oldest spider crabs (4 years old and over) had significantly higher $\delta^{13}C$ ratios than the juvenile ones (0-1 and 1-2 years old), and they also exhibited enriched nitrogen values compared to all the other age classes (Tukey-Kramer test, $p<0.05$). In the Seine Bay population, all individuals had similar stable isotopic signatures, except the 0-1 year old juveniles which were significantly depleted in nitrogen (Tukey-Kramer test, $p<0.05$).

3.4. Sex, age and migration effects on isotope ratios in adult spider crabs

A two-way factorial Model I ANOVA was performed on $\delta^{13}C$ and $\delta^{15}N$ data of adult spider crabs, in order to study the influence of sex, age (2 age classes were tested: 3-4 years old and 4 years old and more) and migration (shallow and deep bottoms) (Table 3).

In the Seine Bay, neither the sex, nor the age nor migration had any effect on either the $\delta^{15}N$ or $\delta^{13}C$ values. However, Migration × Age significantly affected the carbon isotopic composition ($p<0.05$). In the Iroise Sea, migration had a significant effect on both $\delta^{13}C$ and $\delta^{15}N$ values, which were lower in specimens collected on shallow bottoms (respectively -16.26 ± 0.62 and 12.20 ± 0.46) than on deep bottoms (respectively-15.15 ± 0.51 and 13.15 ± 0.53) (Tukey-Kramer test, $p<0.0001$) (Fig. 4). Moreover, the nitrogen isotopic ratio was significantly affected by the spider crab's age, with the highest $\delta^{15}N$ values in the oldest specimens (Tukey-Kramer test, $p<0.01$). Finally, the interaction Sex × Age and Migration × Sex × Age significantly affected the nitrogen isotopic composition.

4. Discussion

Maja brachydactyla, like most decapod crustaceans, is opportunistic and consumes whatever range of food is available where it lives (Stevcic 1968, De Kergariou 1974, Bernárdez et al. 2000). Omnivory is a particularly well-suited dietary strategy of migratory crustaceans which are likely to encounter a wide variety of potential food items while crossing different habitats in the course of their seasonal migrations. Originally, the position of such organisms within food webs and their diet composition were based on direct observations, laboratory experiments and/or gut content analysis. However, these classical approaches often remain critical for opportunistic species in deciding whether observations over restricted time periods are representative of their diet in general. For this reason, stable isotope analysis, which reflects the mean composition of the assimilated diet, is particularly appropriate in the case of omnivorous crustaceans.

The results showed slight but significant differences between the Seine Bay and the Iroise Sea spider crab populations in terms of carbon and nitrogen stable isotopic composition. The Seine Bay population had enriched values for both $\delta^{13}C$ and $\delta^{15}N$. Moreover, ontogenic variations in the spider crab muscle stable isotopic composition followed different patterns in the two sampling areas, except for the sex parameter. In spite of the morphological dissimilarity of their chelipeds and their different energetic demands, the males and females in this study did not present any significant differences in isotopic signatures, whatever the age and the migration period, for both spider crabs from the Seine Bay and the Iroise Sea. A similar result was obtained by Bernárdez et al. (2000) in spider crab gut contents from Galicia (Spain), whereas De Kergariou (1974) found a significant sex effect by studying both direct spider crab behaviour in the field and gut contents, for specimens from Brittany (France). The large $\delta^{13}C$ and $\delta^{15}N$ standard deviations observed in males and females of different age classes in both sampling areas confirm the opportunistic behaviour of the spider crab, which probably conceals slight isotopic differences due to sex. However, results of this study highlighted significant differences between the two populations focused on with respect to the influence of ontogenic factors such as age, size and seasonal migration. Indeed, while specimens from the Seine Bay presented low variability both for $\delta^{13}C$ and $\delta^{15}N$, the carbon and nitrogen isotopic signatures in spider crabs from the Iroise Sea were strongly influenced by all these parameters.

Like other *majidae*, but contrary to the majority of decapod crustaceans, *Maja brachydactyla* grows only during its two-year juvenile stages (Le Foll 1993). Therefore, age and body size are correlated only during the juvenile stage, and especially during the first year of life. A spider crab adult aged 4 years and more can be smaller than those of 2-3 or 3-4 years old, and even some juveniles of 1-2 years old (Le Foll 1993). In the Iroise Sea spider crab population, the study of the variations in carbon and nitrogen isotopic ratios in the muscle revealed an increase in the values with size, as well as with the age of the specimens. The $\delta^{13}C$ and $\delta^{15}N$ differences between the youngest (0-1 year old) and the oldest (4 and more years old) were respectively1.3‰ and 1.0‰, while the $\delta^{13}C$ and $\delta^{15}N$ enrichments between the smallest (CL = 50-70 mm) and the largest (CL > 170 mm) specimens were 2.6‰ and 1.5‰, respectively. These $\delta^{13}C$ and $\delta^{15}N$ values in the largest and oldest cohorts which are higher than in the smallest and youngest ones suggest a change in feeding habits. Different authors have suggested that a mean enrichment in $\delta^{13}C$ and $\delta^{15}N$ of about 0-1‰ and 3-4‰ respectively, from a prey to its consumer can be admitted (De Niro & Epstein 1978, 1981, Minagawa & Wada 1984, Peterson & Fry 1987, Post 2002). However, Yokoyama et al. (2005) argued that the fractionation is species- and tissue-specific and that the classical diet-tissue carbon isotopic fractionation is not applicable to all animals and/or ecological systems. In particular, they demonstrated that crustacean muscles have a larger ^{13}C fractionation than the currently accepted fractionation of 0-1‰. For example, ^{13}C fractionations for the callianassid shrimp and prawn muscles were estimated at 2.0-2.2‰ and 1.7‰, respectively (Parker et al. 1989; Yokoyama et al. 2005). Taken these enrichment values into consideration as valid references for the spider crab (2‰ and 3-4‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively), ageing would not lead to any determining trophic shift (for both $\delta^{13}C$ and $\delta^{15}N$) in the Iroise Sea population. It could be deduced that the spider crab remains on one trophic level throughout its life. However, significant ^{13}C enrichment between the smallest and the largest specimens reveals a shift towards “benthic-component” prey (Hobson et al. 1995, Le Loc’h & Hily 2005). Finally, spider crab growth (in term of relative size and weight) seems to be a more important factor for feeding habit changes than ageing.

In literature, no differences with body size in spider crabs' diet were found by Hartnoll (1963) and De Kergariou (1974). On the contrary, during laboratory experiments, inclusion of Rhodophyceae in tanks used for juvenile *Maja brachydactyla* improved survival rates (Le Foll 1993), whereas adult spider crabs have been successfully maintained in aquariums using diets from which plant material was entirely absent (Brosnan 1981). Moreover, Bernárdez et

al. (2000) observed changes in gut contents between juvenile and adult specimens collected in summer in the Ría Arousa. They concluded that diet is slightly diversified for juvenile spider crabs probably due to the demand for certain nutrients required during the moulting period. The stable isotope results obtained in this study confirm those of these previous studies, considering that a diet mainly based on primary producers (macro-algae) will generate a lower mean $\delta^{15}N$ signature than a diet based on secondary producers (polychaetes, molluscs and echinoderms).

Moreover, $\delta^{15}N$ values in spider crab muscles from the Iroise Sea showed a slight decrease between the 1-2 year old and the 2-3 year old classes, followed by an increase up to the oldest age class. The sharpest drop occurred in the year of the pubertal moult, when juvenile spider crabs attain sexual maturity and then migrate to deep bottoms for the first time. In the Iroise Sea, the nursery area and coastal spawning zone of adult spider crabs are two distinct biotopes: the nursery is an infralittoral seagrass habitat in sandy sediment, while the adults are localised on kelp beds in rocky areas. This biotope change influences the isotopic signatures of the newly-moulted adults by a quantitative and qualitative change in available prey (primary and secondary producers).

Offshore, the biotopes in which the adult spider crab population from the Iroise Sea spends the autumn and winter periods are very different in terms of habitat and associated communities. Indeed, *Maja brachydactyla* have no macrophytes available for consumption and its diet is only based on invertebrates from various trophic levels of the coarse sand community present in this area (Raffin, 2003). The $\delta^{13}C$ and $\delta^{15}N$ seasonal differences in adult spider crab muscles between summer/coastal and winter/offshore periods were respectively 1.1‰ and 1.0‰. These significant increases from coastal to offshore bottoms during migration can be explained by diet changes induced by the differences between infralittoral communities and coastal communities. Bernárdez et al. (2000) also found a seasonal difference in the diet of *Maja brachydactyla* from Galicia (Spain), by studying gut contents. If the spider crab is really an opportunistic feeder, then the isotopic values will reflect the levels of the prey which are most accessible and predominant in the biotope. If migration involves one or more biotope changes, the available prey will change and will probably not show the same levels in terms of $\delta^{13}C$ and $\delta^{15}N$. Raffin (2003) identified four different communities over the whole area concerned by the spider crab migration in the Iroise Sea. In addition, differences in $\delta^{13}C$ and $\delta^{15}N$ among coastal and more open-water habitats may result from different C and N inputs and availabilities but also from various

physical processes (ocean currents, wind, tides) of these two marine ecosystems (Riera et al. 2000, Sherwood & Rose 2005).

Contrary to the Iroise Sea population, very slight variations in the carbon and nitrogen stable isotopic signatures were noted in the spider crabs from the Seine Bay. Only $\delta^{15}N$ was found to increase significantly with size. The $\delta^{15}N$ enrichment between the smallest (CL = 35-50 mm) and the largest (CL > 140 mm) specimens was 0.9‰, which corresponds to a slight trophic level increase and is lower than that of the spider crabs from the Iroise Sea. Moreover, all age classes presented similar isotopic ratios, except the youngest spider crabs which had slightly lower but significant $\delta^{15}N$ values compared to the others (difference of 0.85‰). Finally, no significant differences were observed for either carbon or nitrogen between the summer/coastal and the winter/offshore samples. This stability of isotopic values observed in the Seine Bay can be explained by the homogeneity of the habitat and associated communities over the entire area. Indeed, the authors who described the sediments and invertebrate communities of this zone (Gentil, 1976; Olivier and Retière, 1998), showed that the whole area (from inshore to offshore) is composed of gravels and heterogeneous coarse sediment associated with only one community. The only clear change in terms of sediment and community occurs in the very shallow waters where sediments are muddy fine sands, which only concern the first stages of juveniles. The results agree with this point since all age classes presented similar isotopic ratios, except for the youngest spider crabs, living exclusively in these shallow muddy sands, which had slightly lower but significant $\delta^{15}N$ values compared to the others. So the Seine Bay population appears on the whole as being very stable for carbon and nitrogen stable isotopic signatures.

Finally, the differences between the two populations should reveal the strong differences in the two geographic areas in terms of heterogeneity of the biotopes concerned by the benthic life cycle of the spider crabs. These differences between different populations can be masked if the demographic structure is not considered. Indeed, an overall comparison of the two series of samples, even if the statistics showed significant differences, gave much closer results both in term of carbon and nitrogen. Consequently it is strongly recommended to analyze size classes separately.

To our knowledge, very few studies have investigated the ontogenic variations in stable isotopic signatures in benthic decapod crustaceans. For example, Le Loc'h & Hily (2005) studied trends in the carbon and nitrogen isotope signatures with size in the Norway lobster (*Nephrops norvegicus*) and the squat lobster (*Munida sarsi*) from the Bay of Biscay (France).

These two omnivorous crustaceans, like *Maja brachydactyla*, change their diet as they grow. Moreover, Sherwood & Rose (2005) observed significant higher $\delta^{15}N$ values in the brown shrimp (*Pandalus borealis*) and the snow crab (*Chionoecetes opilio*) from offshore habitats (>200 km offshore) of the Newfoundland and Labrador continental shelf ecosystem. They also highlighted lower carbon isotope signatures in *Pandalus borealis* from near-shore areas (<2 km from shore). All these findings reveal that the stable isotope approach has proved successful in investigating trophic behaviour of omnivorous crustaceans, and especially for accurately assessing ontogenic variations in their feeding habits.

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Table and figure list

Table 1. Mean $\delta^{13}C$ and $\delta^{15}N$ values (‰) and standard deviation of spider crabs muscle tissue from the Seine Bay and the Iroise Sea. CL = carapace length (in mm), W = total fresh weight (g).

Sampling area	Sex	Age	Shallow waters					Deep waters				
			n	CL (mm)	W (g)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	n	CL (mm)	W (g)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Seine Bay	Male	0-1	8	55 ± 15	54 ± 43	-15.01 ± 0.48	12.3 ± 0.71					
		1-2	12	95 ± 8	251 ± 106	-15.25 ± 1.02	12.92 ± 0.47					
		2-3	4	126 ± 14	839 ± 312	-14.28 ± 1.15	13.04 ± 0.38					
		3-4	4	115 ± 7	515 ± 117	-14.8 ± 0.25	12.58 ± 0.45	4	111 ± 20	372 ± 299	-15.48 ± 0.48	12.76 ± 0.41
		4+	3	109 ± 9	409 ± 167	-15.27 ± 1.12	12.64 ± 1.28	5	119 ± 16	635 ± 257	-14.79 ± 1.29	13.11 ± 0.7
	Female	0-1	8	54 ± 11	50 ± 32	-15.03 ± 0.4	11.88 ± 0.47					
		1-2	12	101 ± 13	328 ± 104	-15.21 ± 0.78	12.92 ± 0.6					
		2-3	3	105 ± 21	326 ± 206	-15.4 ± 0.74	12.90 ± 0.52					
		3-4	15	114 ± 22	484 ± 375	-14.86 ± 0.41	13.04 ± 0.42	7	111 ± 8	442 ± 99	-15 ± 0.42	13.02 ± 0.34
		4+	3	121 ± 16	701 ± 325	-15.41 ± 0.64	13.12 ± 0.66	4	113 ± 6	445 ± 149	-14.77 ± 0.1	13.18 ± 0.51
Iroise Sea	Male	0-1	14	69 ± 8	109 ± 29	-17.47 ± 1.14	12.04 ± 0.48					
		1-2	15	102 ± 12	272 ± 132	-16.38 ± 0.99	12.63 ± 0.38					
		2-3	4	112 ± 10	483 ± 37	-16.81 ± 0.5	12.23 ± 0.53					
		3-4	7	118 ± 17	541 ± 287	-16.52 ± 0.76	12.47 ± 0.41	8	170 ± 17	1610 ± 367	-15.09 ± 0.33	13.27 ± 0.29
		4+	5	147 ± 14	1099 ± 381	-15.55 ± 0.68	13.29 ± 0.36	6	164 ± 19	1551 ± 509	-15.2 ± 0.61	13.11 ± 0.75
	Female	0-1	14	70 ± 8	104 ± 26	-17.07 ± 0.83	12.22 ± 0.6					
		1-2	15	99 ± 11	247 ± 80	-16.58 ± 0.68	12.4 ± 0.38					
		2-3	4	115 ± 9	485 ± 132	-16.23 ± 0.48	12.53 ± 0.71					
		3-4	22	123 ± 12	580 ± 160	-16.1 ± 0.76	12.37 ± 0.62	7	140 ± 10	806 ± 96	-15.68 ± 0.58	12.53 ± 0.46
		4+	6	124 ± 11	627 ± 191	-16.21 ± 0.43	13.03 ± 0.46	4	138 ± 6	833 ± 107	-15.71 ± 0.4	13.81 ± 0.26

Table 2. Results of two-way ANOVA on muscle stable isotopes data in spider crabs from the coastal waters. ns = not significant.

Sampling area	Effects	*df*	$\delta^{15}N$		$\delta^{13}C$	
			F	*p-value*	*F*	*p-value*
Seine Bay	Sex	1	0.15	ns	1.19	ns
	Age	4	7.95	<0.0001	0.58	ns
	Sex × Age	4	1.30	ns	1.08	ns
Iroise Sea	Sex	1	0.01	ns	0.02	ns
	Age	4	14.16	<0.0001	15.46	<0.0001
	Sex × Age	4	2.39	ns	1.46	ns

Table 3. Results of two-way ANOVA performed on muscle stable isotopes data in adult spider crabs. ns = not significant.

Sampling area	Effects	*df*	$\delta^{15}N$		$\delta^{13}C$	
			F	*p-value*	*F*	*p-value*
Seine Bay	Sex	1	2.62	ns	0.1	ns
	Age	1	0.66	ns	0.01	ns
	Migration	1	0.78	ns	0.1	ns
	Sex × Age	1	0.05	ns	0.34	ns
	Migration × Sex	1	0.58	ns	0.57	ns
	Migration × Age	1	0.23	ns	4.46	<0.05
	Migration × Sex ×Age	1	0.07	ns	0.17	ns
Iroise Sea	Sex	1	0.48	ns	3.40	ns
	Age	1	19.27	<0.0001	0.98	ns
	Migration	1	6.93	<0.05	14.01	<0.0001
	Sex × Age	1	4.71	<0.05	1.86	ns
	Migration × Sex	1	0.30	ns	1.39	ns
	Migration × Age	1	0.38	ns	1.89	ns
	Migration × Sex ×Age	1	7.21	<0.01	2.56	ns

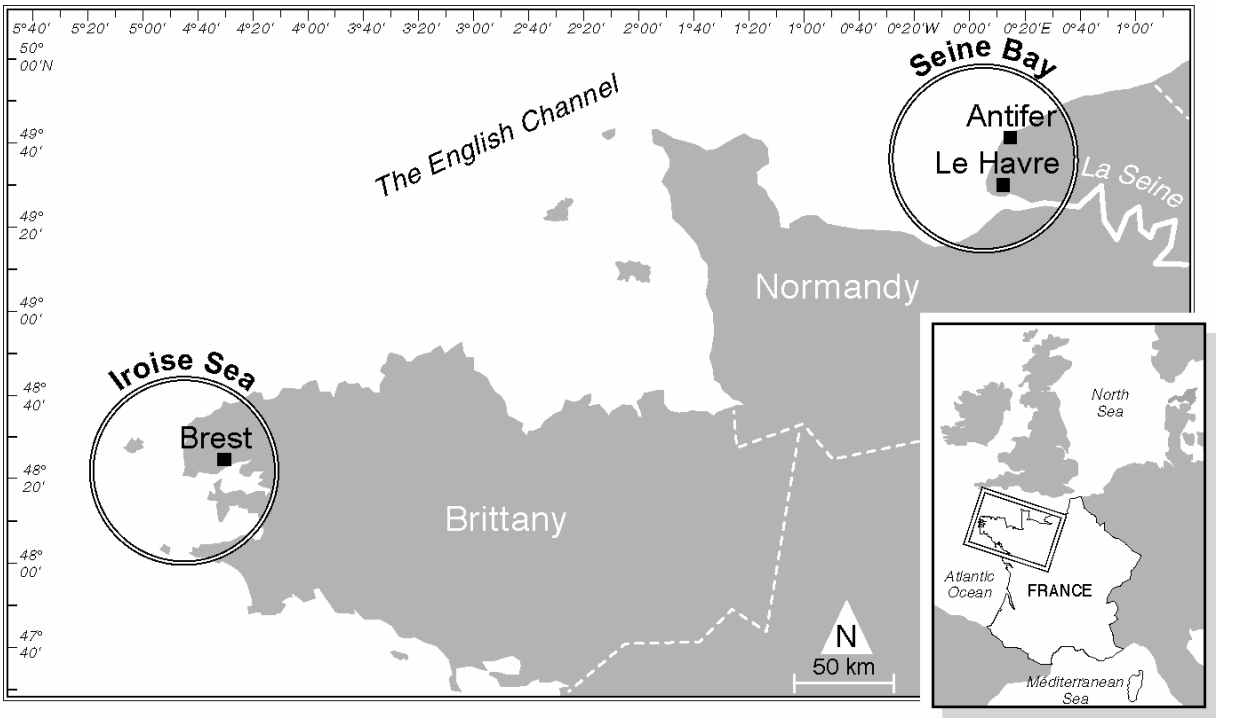

Fig. 1. Map of the two sampling areas: Iroise Sea and Seine Bay

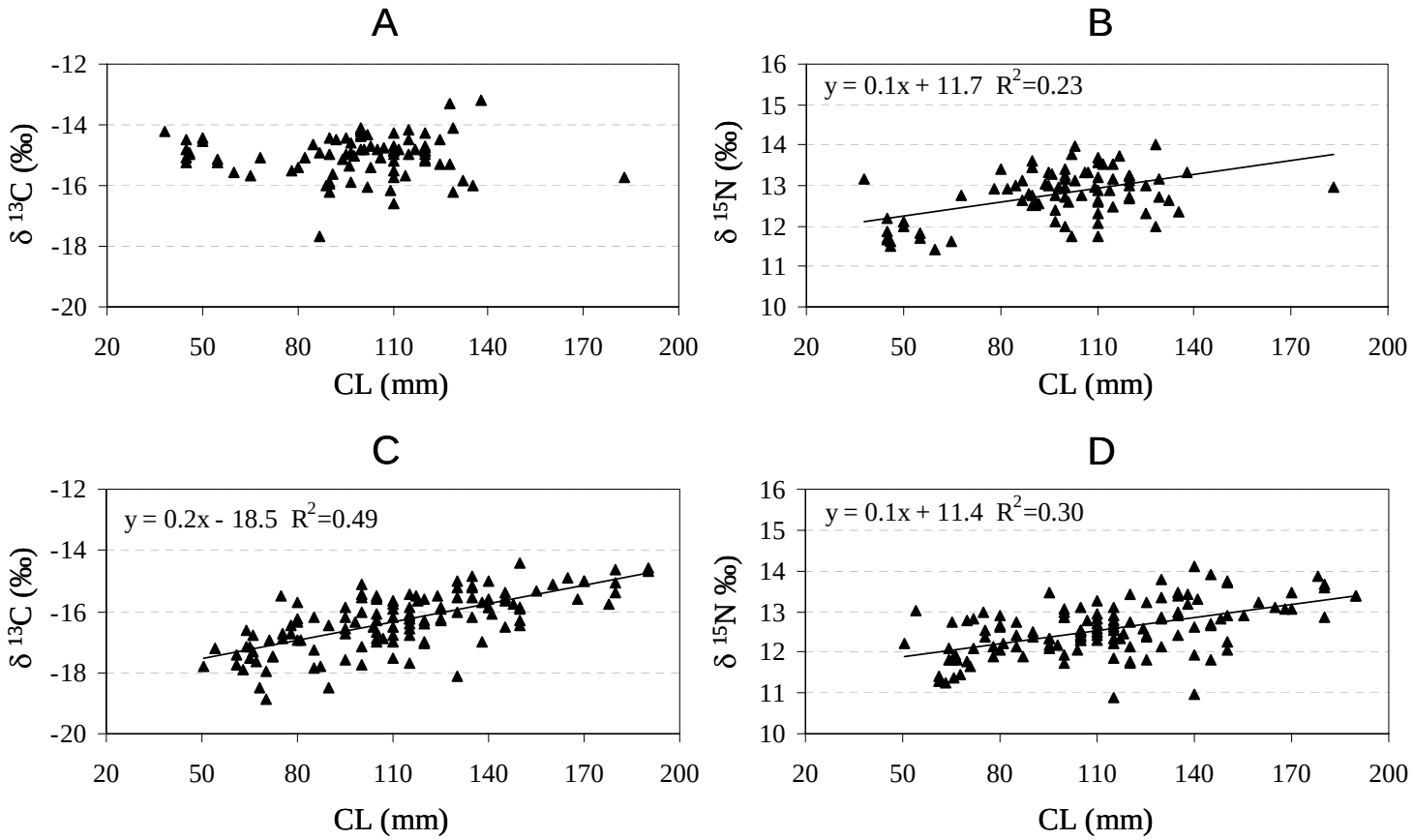

Fig 2. Relationships between carapace length (CL) and spider crab muscle tissue from the Seine Bay (n=92) for $\delta^{13}C$ (A) and $\delta^{15}N$ (B) and from the Iroise Sea (n=131) for $\delta^{13}C$ (C) and $\delta^{15}N$ (D).

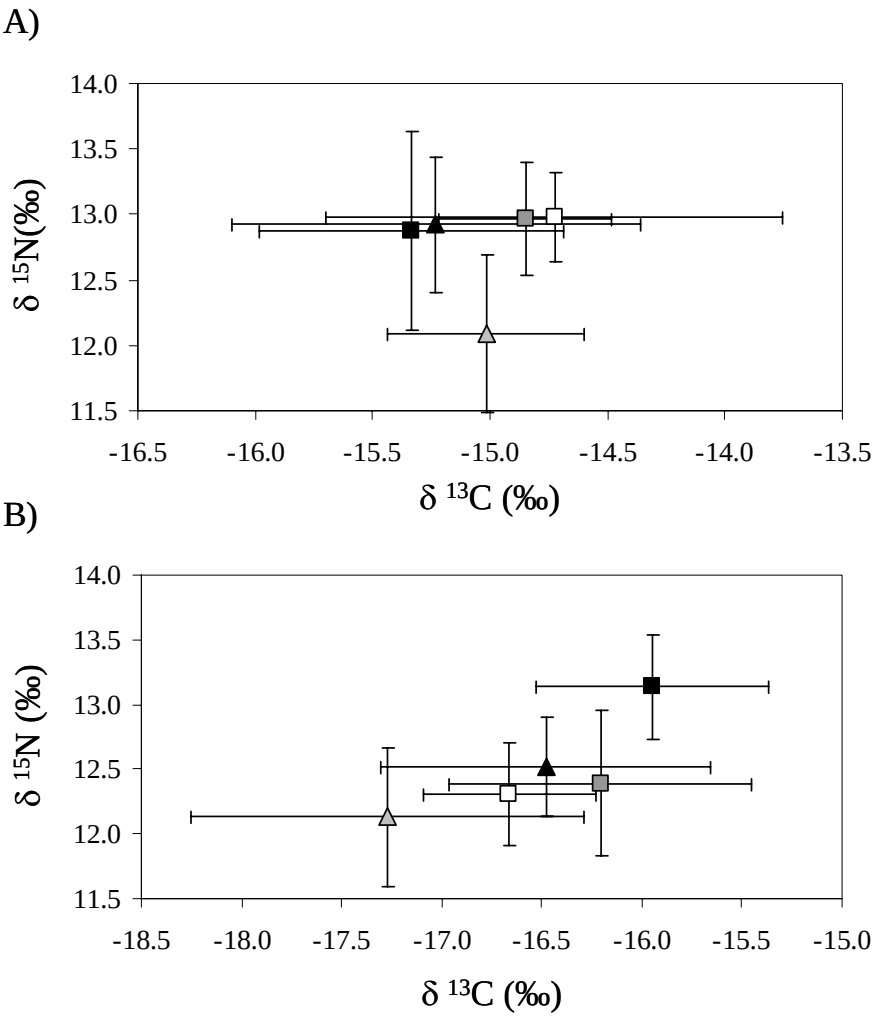

Fig. 3. Distribution of carbon and nitrogen stable isotope ratios (mean ± SE) among age groups of spider crabs from the Seine Bay (A) and the Iroise Sea (B), collected in coastal waters. △ = juvenile individuals of 0-1 years old (A: n = 16; B: n = 28); ▲ = juvenile individuals of 1-2 years old (A: n = 24; B: n = 30); □ = adult individuals of 2-3 years old (A: n = 7; B: n = 8); ■ = adult individuals of 3-4 years old (A: n = 19; B: n = 29); ■ = adult individuals of 4 years and more (A: n = 6; B: n = 11).

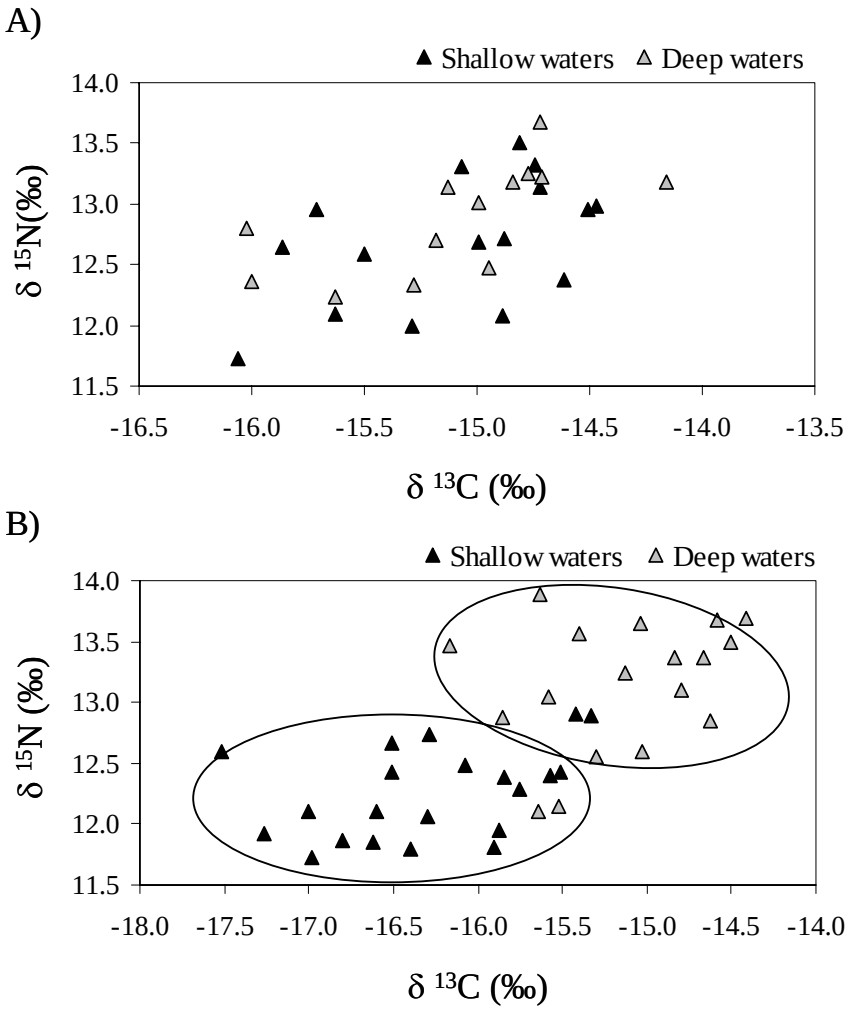

Fig. 4. Distribution of $\delta^{13}C$ and $\delta^{15}N$ in the muscle tissue of male and female adult spider crabs (3-4 years old) collected in deep and shallow waters from the Seine Bay (n = 30) and the Iroise Sea (n = 40).