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Growth and reproduction of the common whelk *Buccinum undatum* in west Cotentin (Channel), France

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Abstract – The common whelk *Buccinum undatum* (Neogastropoda, Buccinidae) is widespread along the north Atlantic coasts of France. In west Cotentin (Normandy), an important local fishery exists that depends exclusively on this marine resource and represents about 90% of French whelk production. Despite successive restrictive measures, fishing yields have decreased since 2000. Shell length frequency distributions of *Buccinum undatum* caught in west Cotentin were studied in 2005 ($N = 2910$), in 2007 ($N = 2032$) and in 2009 ($N = 4145$) ranging from 7 to 85 mm. In order to preserve this fishery and to characterise the whelk stock at this site, the reproductive biology of this species was studied in relation to age, sex and size, for whelks of commercial size (45 to 61 mm) over the complete annual cycle in 2008. Age was determined by reading the number of operculum striae: animals between 45 and 59 mm had 2 to 4 striae. Four reproductive stages were defined for males and females on the basis of histological analysis. The time course of reproductive events was described according to size and sex: the highest percentages of ripe stages were found in October for both sexes. Spawning events occurred between October and December. The shell length that corresponded to 50% of animals having mature gonads (49 mm and 52 mm for males and females, respectively, corresponding to 3 and 4 years old animals) exceeded the minimal landing size (45 mm). Fifty percent maturity was reached for males in their third year and for females in their fourth year. Reproductive investment was evaluated by quantitative analysis of the gonadal thickness or surface and was found to be proportional to shell size. We found that less than 20% of females under 49 mm in length were sexually mature and that these produced only a few eggs. This information, collected in a major fishing area, should assist fishery management decisions.

Key words: Fishery survey / age / size at sexual maturity / reproductive cycle / Mollusc Gastropoda / *Buccinum undatum* / NE Atlantic

1 Introduction

The common whelk *Buccinum undatum* L. is widely distributed on both sides of the Atlantic, from south Canada to New Jersey in North America and from Norway to France in Europe.

This species is widely distributed in coastal areas of the northern Atlantic Ocean (Golikov 1968). *Buccinum undatum* is a neogastropod mollusc that lives mainly in the zone from low tide level to 200 m, and occasionally at depths ranging between 400 and 1400 m on various substrates (Mercier and Hamel 2008). *B. undatum* is described as a predominantly scavenging species, living on a diet mainly composed of bivalves and polychaetes. This species is gonochoric, with a sexual dimorphism based on the presence of a penis in males and distinctive sexual glands in both sexes. The course of the reproductive cycle and the duration of mating are highly variable according to location. In eastern Canada, whelk testis and ovary were found to display a differential development with long-term storage of sperm in the seminal vesicle of the male prior to copulation, and egg laying was seen to occur from late May to July in relationship with

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increasing water temperature (Martel et al. 1986; Himmelman and Hamel 1993). For European populations, gonad maturation takes place during the spring and summer whereas egg laying occurs during the winter, as established from the observation of fixed eggs on fishing pots (Santarelli-Chaurand 1985; Valentinsson et al. 1999). Fertilization is internal and eggs are contained within capsules laid on hard benthic substrates. Development takes place inside the egg capsules and hatching of juveniles occurs after 3 to 8 months (Santarelli-Chaurand 1985; Martel et al. 1986 and pers. obs.).

In 2008, France was the second largest producer of whelks (behind UK) in the northeast Atlantic, responsible for about 42% of total catches (12 000 t, 2008 FAO data). The most important fishing site is located in the west Cotentin area (Santarelli and Gros 1984; Santarelli-Chaurand 1985) and Granville harbour is the main centre for whelk sales in France.

The local official production reached 6250 tons and 9560 k€ in 2008 (Ifremer data, SIH 2008). This fishery concerns 75 boats, each with 2 or 3 fishermen aboard. Whelks are collected in pots (45 cm in diameter with 2 cm holes at the bottom allowing the smallest animals to escape); each boat collects 480 to 720 pots (by lines of 40 to 60 pots) per day. Market-sized whelks were then sorted from the others on board, using grids to select animals longer than 45 mm.

One of the measures taken to protect this species from overfishing is the definition at the EU level of a minimal landing size (MLS) set at 45 mm shell length. This limit is based on the size associated with 50% of animals with mature gonad (L_{50}). However, data on whelks have confirmed large variations in size at first sexual maturity, which is related to water temperature. Due to the growth and reproductive performances of whelks, this MLS was locally increased from 45 to 75 mm around Shetland (Henderson and Simpson 2006; Shelmerdine et al. 2007). In the Channel area, L_{50} was estimated between 45 and 50 mm shell length in the Normand-Breton Gulf (Santarreli and Gros 1985). Therefore, the minimal landing size of 45 mm seemed to fit the conservation guidelines and was applied on French coasts from 1995. However, recent investigations of the evolution of the whelk population around the Jersey in the Channel Islands (west Cotentin coasts) highlighted local variations in the L_{50} (Morel and Bossy 2004). On the basis of catch per unit effort (CPUE) comparisons between a fished sampling station and a non fished sampling station, these authors reported that the populations were differentially structured at the two sites, suggesting that fishing may cause sexual maturity to be reached at a smaller size. The possible influence of fishing on the evolution of L_{50} should therefore be taken into account for fisheries management. Moreover, Martel et al. (1986) noticed that, in the northern Gulf of St. Lawrence (Canada), males reached sexual maturity at a slightly smaller size than females. This suggests that MLS should be increased to adapt it to female L_{50} and thus increase protection of maturing females.

In the area of Granville in west Cotentin, where this species has been commercially harvested, additional restrictive measures have been progressively established to compensate for the diminishing yields observed since 2000. According to these guidelines, whelks must be sorted on board and animals below the size limit must be returned to the sea. Fishing days are limited, the number of fishing licenses is being progressively reduced and, since 2009, fishing in January has been suspended.

In order to provide information to facilitate whelk stock management and to ensure the sustainability of the resource, a survey procedure was initiated in 2005, consisting of evaluating size distribution of the population every two years. In addition, to obtain detailed information on the reproductive biology of whelks of commercial size in west Cotentin, a qualitative and quantitative histological analysis of the reproductive cycle was performed over a whole year (2008). We linked this analysis to biometric data to determine the size, weight and age at which animals became sexually mature. Males and females were treated separately so as to detect any differences between the sexes in reproductive timing.

2 Materials and methods

2.1 Biological material

Animals were collected in whelk pots (line of 40 to 60 pots) on various substrates (sand, mud or hard ground) in the fishing area (Fig. 1), without sorting by professional fishermen. For the study of size frequencies, three successive samplings were performed in the years 2005 ($N = 2910$), 2007 ($N = 2032$) and 2009 ($N = 4145$). Water temperatures were measured twice a month in the same area (hydrobiological network HYDRONOR – SMEL) (Fig. 2). Animal size was recorded individually. For the analysis of reproductive parameters, animals were harvested every two months during 2008, limiting sampling to commercial whelks with shell lengths ranging between 45 mm to 61 mm. Preliminary observations had confirmed that gonadal maturation was scarce among animals under 45 mm shell length, and animals larger than 61 mm represented only 7% of the population. Within this sampled group, eight size classes of 2 mm each were defined: from 45 to 47 mm (called 45), up to 59 to 61 mm (called 59). For each size class, twenty animals were analyzed ($n = 160$ for each of the six sampling dates). Sampling was performed every two months (Feb., Apr., Jun., Aug., Oct. and Dec.) and the animals examined by making biometric measurements, age determination and histological analysis of gametogenesis. The phenotypic sex of animals was determined on the basis of the observation of external sexual dimorphism (Martel et al. 1986).

2.2 Biometric measurements

Total shell length, shell width, total weight, soft body weight and visceral mass weight were recorded individually for each animal at each sampling date. Length-weight relationship was expressed as follows:

$$W = a\,L^b$$

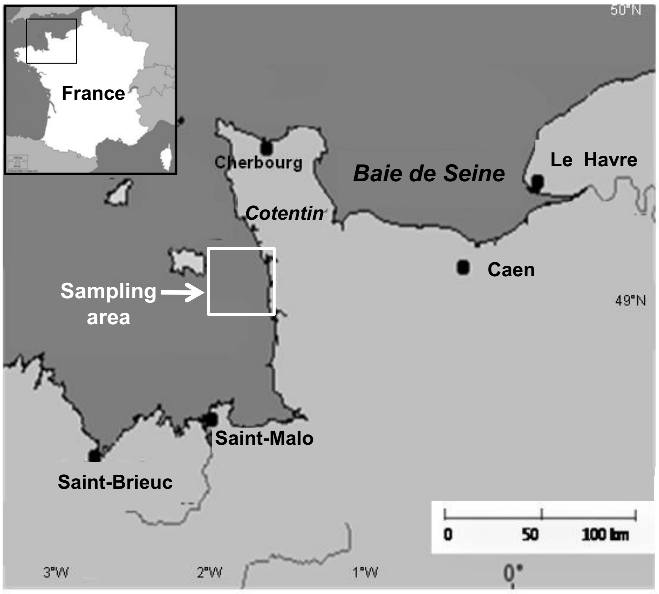

Fig 1. Whelk fishing area in west Cotentin (Normandy). The area of interest is indicated by a box.

where W is the total weight (shell and flesh wet weight, g), L the shell length (mm) and a and b the initial growth coefficient and the relative growth rate, respectively. Calculations were made using linear regression after the log transformation for variables (Narvarte 2006).

2.3 Age determination

Age was estimated by counting the number of dark operculum striae. This approach was validated for *Buccinum undatum* by oxygen isotope analysis (Santarelli and Gros 1985) and has already been used by several authors for various *Buccinum* species (Kideys 1996; Ilano et al. 2004; Narvarte 2006; Shelmerdine et al. 2007). To apply this method, opercula were collected during the sampling, carefully cleaned in order to discard any remaining muscle particles, rinsed, individually stored in 24 well titer plates and dried in an oven at 60 °C before reading. In order not to bias the interpretation of the operculum striae readings, only opercula showing clear striae were retained for the analysis. The age of the animal was reported as the number of dark striae between the nucleus and the opercular edge.

The relationships between age and shell length or age and total weight were fitted with the von Bertalanffy (1938) growth functions to determine growth parameters (Ricker 1975), an approach that has already been validated for *Buccinum undatum* (Kideys 1996; Shelmerdine et al. 2007).

Length (mm) at age equation:

$$L_t = L_\infty\,(1 - e^{-k(t-t_0)})$$

where L_t is the length at age t, k is the growth rate coefficient and t_0 is the hypothetical age at which the length would be zero.

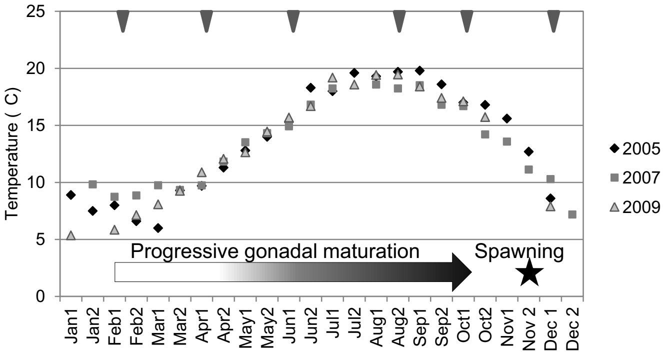

Fig 2. Water temperature variation in the area of interest during the study period (hydrobiologic network HYDRONOR – SMEL). Temperatures were measured in the first week (1) and the middle (2) of each month. Sampling dates in 2008 are indicated by arrowheads.

Body weight (g) at age equation:

$$W_t = W_\infty\,[1 - e^{-k(t-t_0)}]^b$$

where W_t is the weight at age t, W_∞ is the asymptotic weight and b is obtained from the growth-length relationship.

2.4 Histology

Twenty animals of each of the eight size classes were extracted from their shells and carefully rinsed with seawater. Phenotypic sex was determined according to the presence of a penis. The visceral mass was then cut from the muscular mass of foot and fixed in Davidson's solution (10% glycerol, 20% formaldehyde, 30% ethanol 95%, 30% sterile sea water) for 48 h. Pieces were then dehydrated and a transverse section was made through the visceral twist at the same level for all animals. One half turn was embedded in paraffin wax. Sections of 5 µm were prepared for subsequent staining using the Prenant-Gabe trichrome method (Gabe 1968). The determination of sex and stage of gametogenesis was based on microscopic observation (Nikon Eclipse 80i coupled to a Nikon DXM1200-C camera).

2.5 Quantitative measurement of gonad development

Measurement of gonad development was performed using two different quantitative approaches. For all animals (whatever the sex, size and stage of maturity), the gonadal thickness was measured on histological sections cut in the same position on all animals. A mean value was obtained from three measurements made on histological sections in the thickest region of the gonad. In addition, for mature females at stage III gametogenesis only, histological sections were scanned (SupercoolScan 9000, Nikon) and the gonadal surface and the total surface were measured in pixel² (px²) using an application developed with Aphelion software (ADCIS). A gonadal index was calculated as the ratio of the gonadal surface over total surface.

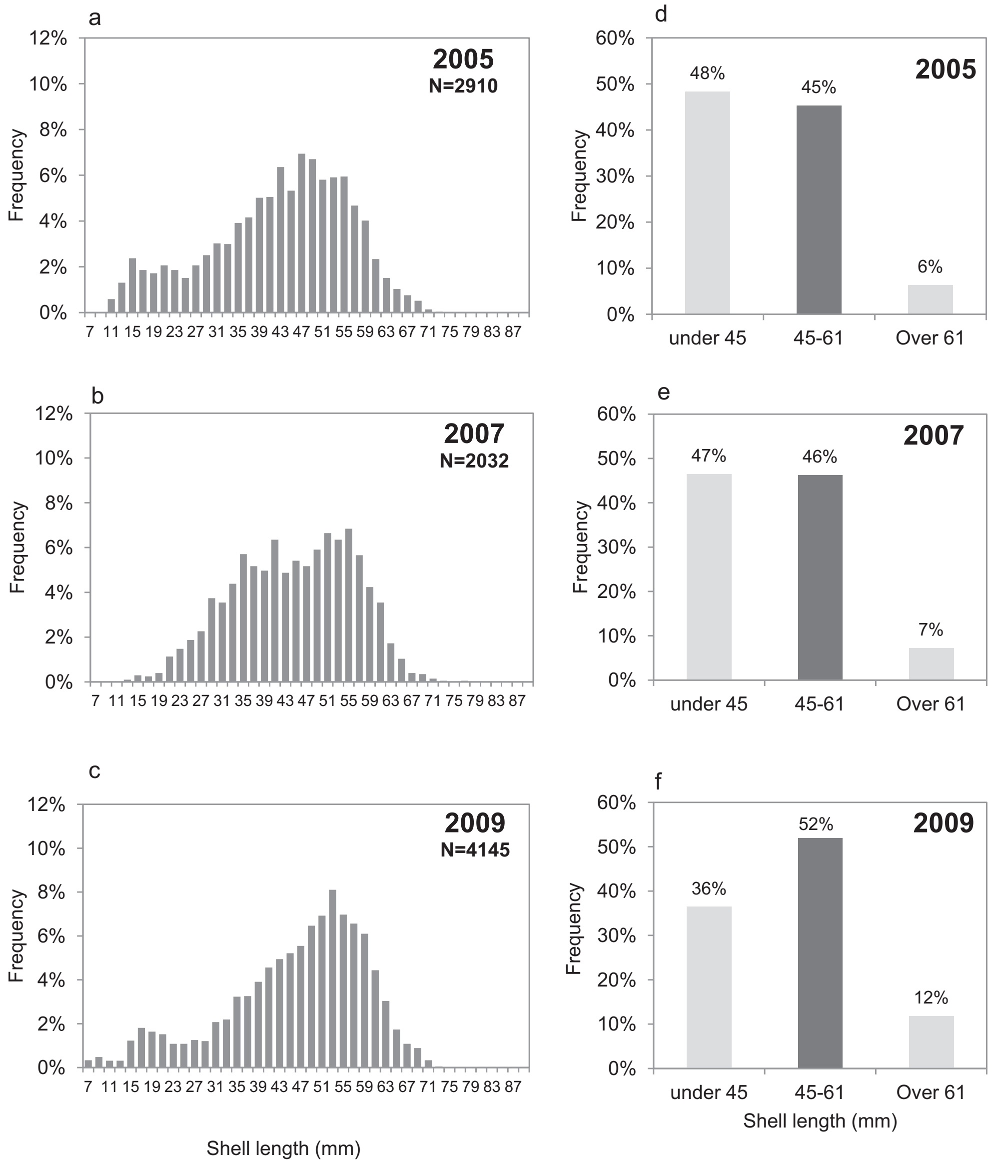

Fig 3. Shell length frequency distribution of *Buccinum undatum* caught in west Cotentin in the following years: a: 2005 ($N = 2910$); b: 2007 ($N = 2032$) and c: 2009 ($N = 4145$). Size classes of 2 mm from 7 to 85 mm were considered; d, e, and f illustrate the relative proportions of animals under the minimal landing size (45 mm), over MLS up to 61 mm and over 61 mm, respectively.

3 Results

3.1 Size frequency

Length frequency distributions were displayed for the years 2005 ($N = 2910$), 2007 ($N = 2032$) and 2009 ($N = 4145$), see Figure 3. For the three samplings, the study area showed a length-frequency distribution with a main peak between 25 and 60 mm. During the study period, the trend in the mean size of animals increased and the percentage of whelks under the MLS (45 mm) diminished from 47% in 2007 to 36% in 2009. Over the same period, the percentage of whelks over 61 mm doubled (from 6% in 2007 to 12% in 2009),

3.2 Relationship between length, growth and age

In October 2008, the length-weight relationships for 160 animals from 45 to 61 mm length ranged from 9 to 31 g (total weight). No significant differences were detected between the slopes of the different sexes (parallelism test-ANCOVA); thus males and females fitted the same curve. A linear regression enabled the initial growth coefficient and relative growth rate to be determined. The length-weight relationship was $\log W = 2.955 \log L - 3.842$, i.e., $W = 0.000144\, L^{2.955}$ (Fig. 4a).

The mean numbers of operculum striae for the eight size classes investigated are shown in Fig. 4b. The most frequent size in the population was around 53 mm (2009 data), which corresponded to estimates of 3 or 4 opercular striae.

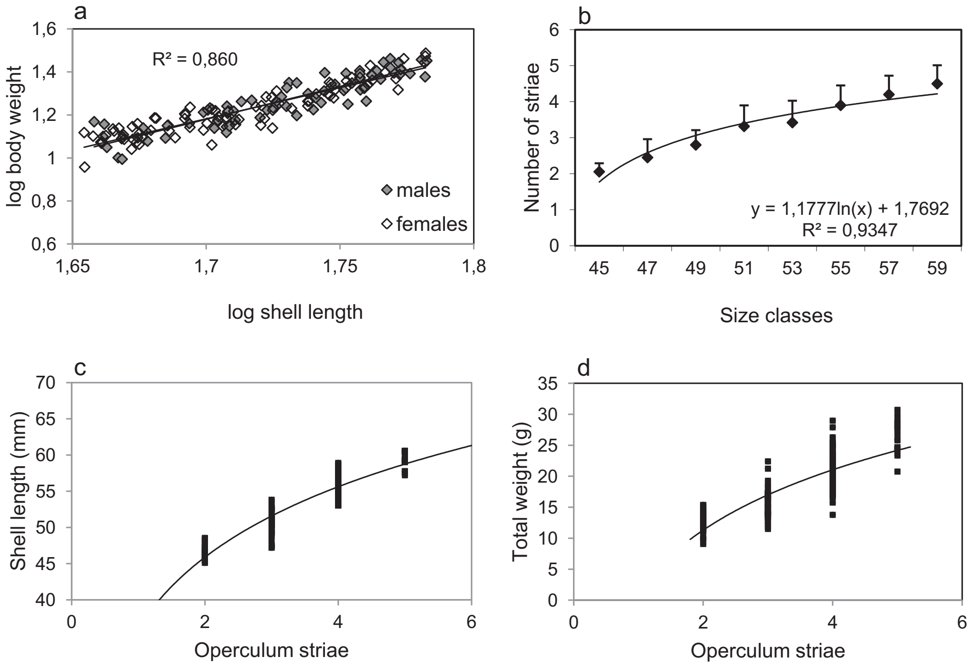

Fig 4. Relationship between length, growth and age for animals sampled in October 2008 ($N = 160$); a: length-weight ; b: mean age of the various size classes from 45 to 60 mm; c: von Bertalanffy growth curve fitted to length data; $L_t = L_\infty (1 - e^{-k(t - t_0)})$; d: von Bertalanffy growth curve fitted to total body weight data; $W_t = W_\infty (1 - e^{-k(t - t_0)})^b$. Length of sampled animals ranged from 45 to 60 mm and weight (tissue + shell) ranged from 9 to 31 g.

Moreover, length and weight-at-age curves (Figs. 4c and 4d) fitted with von Bertalanffy growth functions for length at age and total body weight at age (Table 1).

3.3 Gonadal structure and gametogenesis course

The gonadal area was always seen at the periphery of transverse sections of visceral mass (Fig. 5j), close to the digestive gland. The gonad consists of numerous gonadal tubules (GT) in which germinal cells (GC) can be identified. As gametogenesis progresses, due to the expansion of tubules, the number of tubule sections increases and the appearance of germinal cells changes, allowing the identification of four graded histological stages:

For all sampled animals, the sex determined by phenotypic observation of sexual dimorphism matched with histological sex determination. No cases of imposex (sex difference between external dimorphism and internal gonadal aspect) were observed in our study.

The sex ratio of the whelk population was not statistically different from parity during the sampled period (Chi-square test: $\lambda^2 = 2.2$, $N = 960$).

Stage 0 corresponded to the sexual resting stage for both males and females (Fig. 5). At this stage, gonadal tubules were very restricted and germ cells were scarce. Sometimes, sex identification was not possible on the basis of histological aspect alone. In these cases sexual determination could only be based on phenotypic sexual dimorphism.

Table 1. Growth parameters estimated from operculum striae of *Buccinum undatum* sampled in west Cotentin in October 2008 (von Bertalanffy model). Length of sampled animals ranged from 45 to 61 mm and total weight ranged from 9 to 31 g.

L_∞ (mm)	k	b	W_∞ (g)	N
73	0.221	2.955	45.11	160

Stage I corresponded to the proliferation of germinal cells. Evidence of gonial mitosis was manifest with numerous gonia containing condensed chromosomes in various stages of mitosis (Figs. 5c and 5d). Female gonadal tubules could also contain young previtellogenic oocytes I (Oc).

Stage II was the stage of germinal cell maturation (Fig. 5e and 5f). Males presented the whole germinal lineage including spermatogonia (Spg), spermatocytes (Spc), spermatids (Spd) and spermatozoa (Spz), grouped in islets of cells at the same stage of spermatogenesis. In females, this stage was associated with vitellogenesis and was characterized by the appearance of red-coloured lipid vesicles in the cytoplasm of the maturating oocytes (mOc) and an abundance of somatic intragonadal cells surrounding oocyte islets.

Stage III corresponded to the mature stage in both sexes and was characterized by a large ripe gonad containing mainly mature gametes (Fig. 5g and 5h). In female stage III, the cytoplasm of the oocytes was filled with vitellogenic reserves (lipidic droplets) and intragonadal somatic cells had regressed.

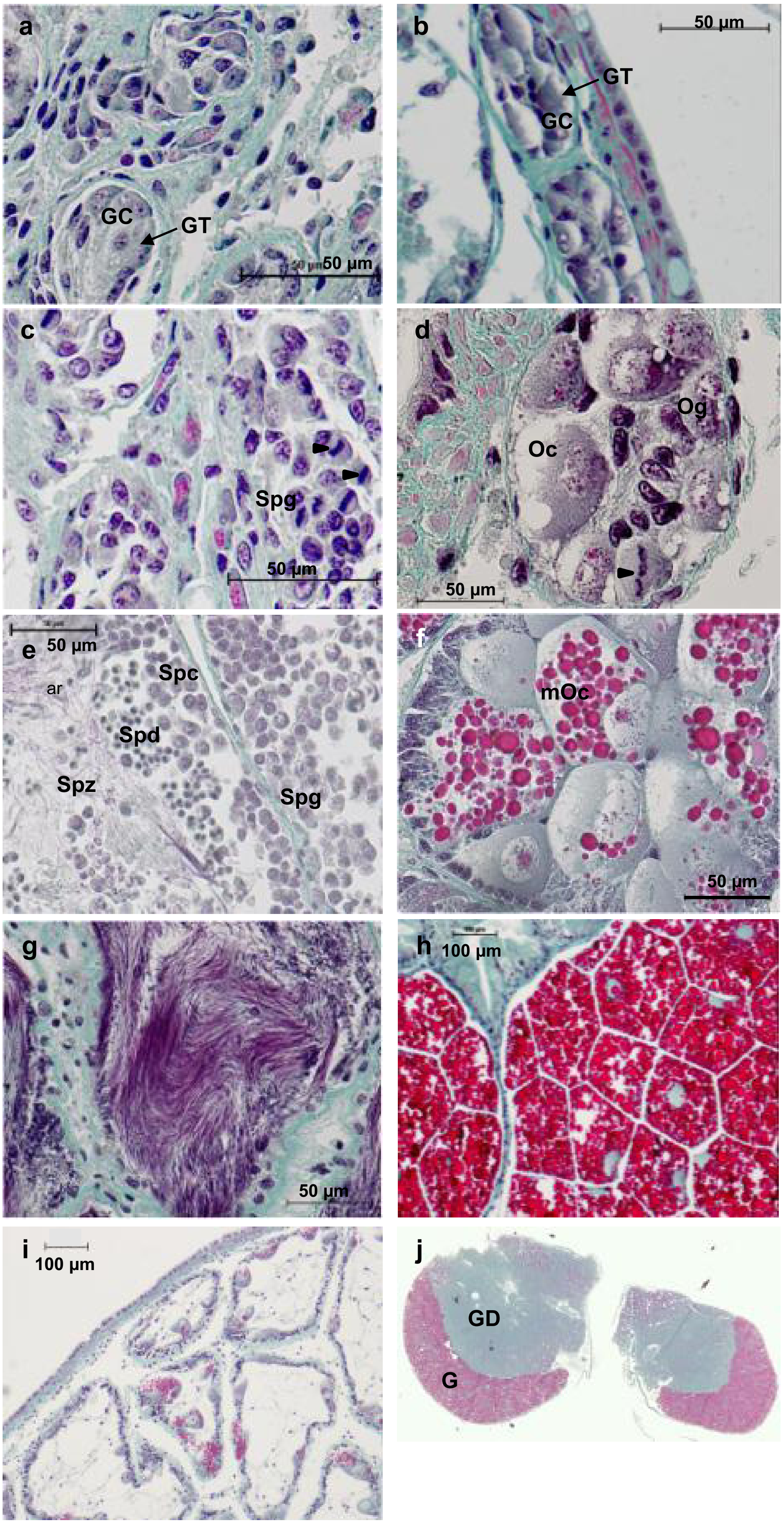

Fig 5. Histological appearance of male and female gametogenesis stages in *Buccinum undatum*; a, b: sexual resting stage (stage 0) for male and female, respectively; c, d: reinitiation of gametogenesis (stage I) for male and female, respectively; e and f: maturation (stage II) for male and female, respectively; g, h: ripe gonad (stage III). i: empty gonad after spawning (stage III); j: localization of the gonad on the transverse section. GT: gonadal tubule; GC: germinal cell, Spg: spermatogonia; Spc: spermatocytes; Spd: spermatide; Spz: spermatozoa; Og: oogonia; Oc: oocytes I; mOc: maturing oocytes I; arrowhead: metaphases stage.

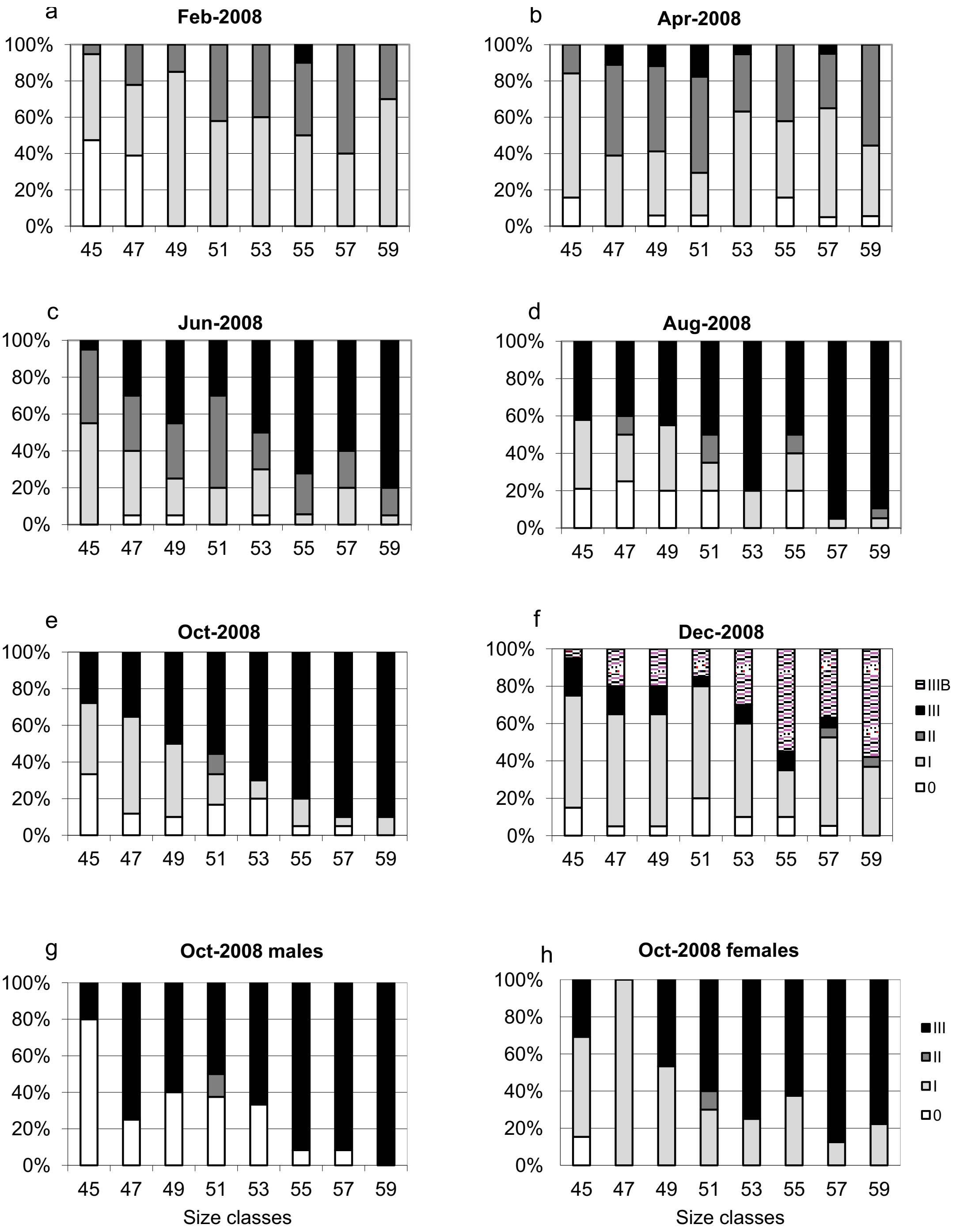

Fig 6. a to f: Distribution of gametogenesis stages for the eight size classes during 2008 (6 sampling dates) without distinction of sexes ($N = 160$ for each sampling date). Stage 0: sexual resting stage; stage I: reinitiation of gametogenesis; stage II: maturation; stage III: sexual maturity; stage IIIB: post spawning animals; g, h: distribution of gametogenesis stages for males and females, respectively, in October 2008 (sexual maturity).

In males, numerous spermatozoa were present and a few spermatids could also be observed.

Stage IIIB was associated with a post-spawning state where gonadal tubules were large and empty (Fig. 5i).

The course of gametogenesis was investigated in relation to the stages defined above for each of the eight size classes ranging from 45 to 61 mm length, every two months in 2008 ($N = 160$ animals for each date, Figs. 6a to 6f). The profiles were not significantly different between males and females, so the sexes were pooled. In some animals, gametogenesis was observed to reinitiate in December just after the spawning event in November. Ripe gonads were occasionally observed in a few

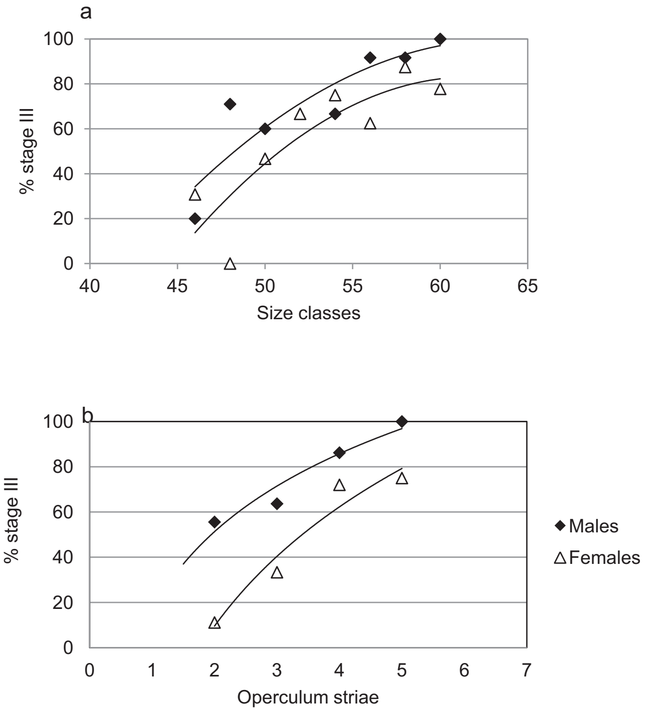

Fig 7. Percentage of mature animals (stage III) in October 2008, in relation to a: shell length; and b: age, expressed as a number of dark operculum striae. Males and females were treated separately.

animals from April. In June, almost 80% of animals belonging to the 59–60 mm size class were already mature, whereas only 5% of the 45–46 size class were in stage III. In this smallest class, a large majority of animals were in stage I at this time. The percentage of stage III increased until October, when more than 90% of animals belonging to 59–60 class size had a ripe gonad but only 30% of the 45–46 size class. In October, the time of year associated with sexual maturity of the gonad, the distribution of gametogenesis stages was detailed separately for males and females (Figs. 6g and 6h). These graphs illustrate that small females (45 to 49 mm shell length) were scarcely mature although gametogenesis had started in most of them (stage I). At this date, males were found to be either sexually mature or at sexual resting stage. In December (Fig. 6f), the relative abundance of stage IIIB indicated that most animals had spawned. However, IIIB stage remained very scarce in the smaller size class (45) suggesting that spawning was unusual for these small whelks.

The percentages of mature animals (stage III) were calculated in October (just before spawning) for males and females of each size class separately. L_{50} was different according to sex: L_{50} was estimated as 49 mm and 52 mm for males and females, respectively (Fig. 7a). Age at sexual maturity was also estimated using the number of operculum striae of mature animals (Fig. 7b). In this way it was shown that 50% males were mature in their third year and 50% of females in their fourth year.

Reproductive investment was assessed by measuring either the thickness of the gonad or the surface on the histological sections. The evolution of gonadal thickness over 2008 was consistent with gonadal maturation, increasing from February to October and decreasing in December after spawning, as illustrated in Figure 8a for the two extreme size classes. The difference between males and females for each size class in October (sexual maturity) showed that gonadal thickness increased with size for both sexes (Fig. 8b). The surface of the gonad and the surface of the total section could only be measured for females due to their histological appearance (Fig. 9). Both surfaces increased with animal size. Moreover, the organ surface was proportional to the total whole body surface on the transverse section (Fig. 9c, no statistical differences between bars, ANOVA test).

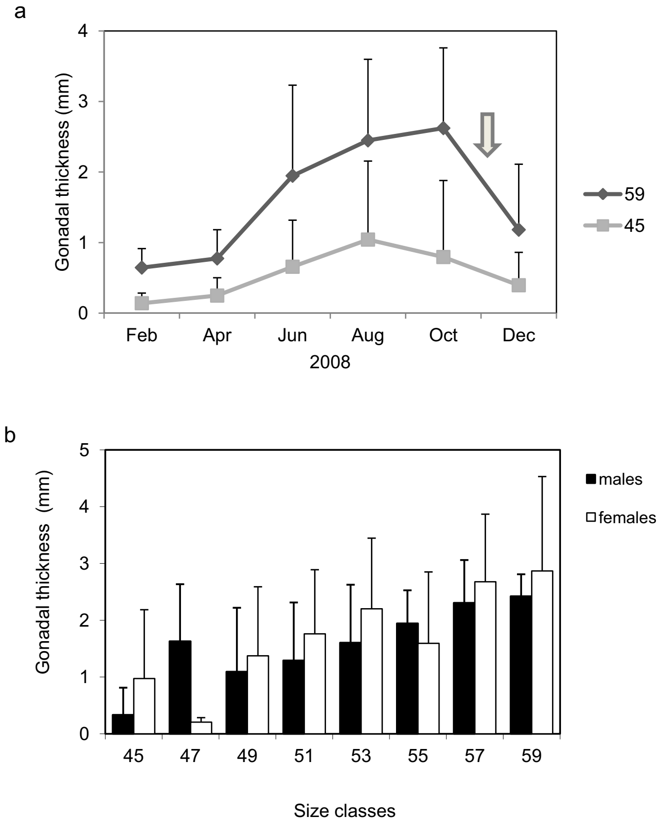

Fig 8. Measurement of gonadal thickness; a: through the year 2008 for the two extreme size classes (45 and 59 mm); b: at maturity in October for males and females separately. Arrow: spawning event; bars correspond to standard deviations.

4 Discussion

As a result of increasing exploitation of *Buccinum undatum* in the west Cotentin area, fishing yields decreased severely from the year 2000, leading the relevance of fishing restrictions to be reconsidered. Subsequently, in addition to the minimal landing size of 45 mm, several more restrictive measures were established. For example, the numbers of fishing days and fishing licenses were limited and whelks were sorted on board

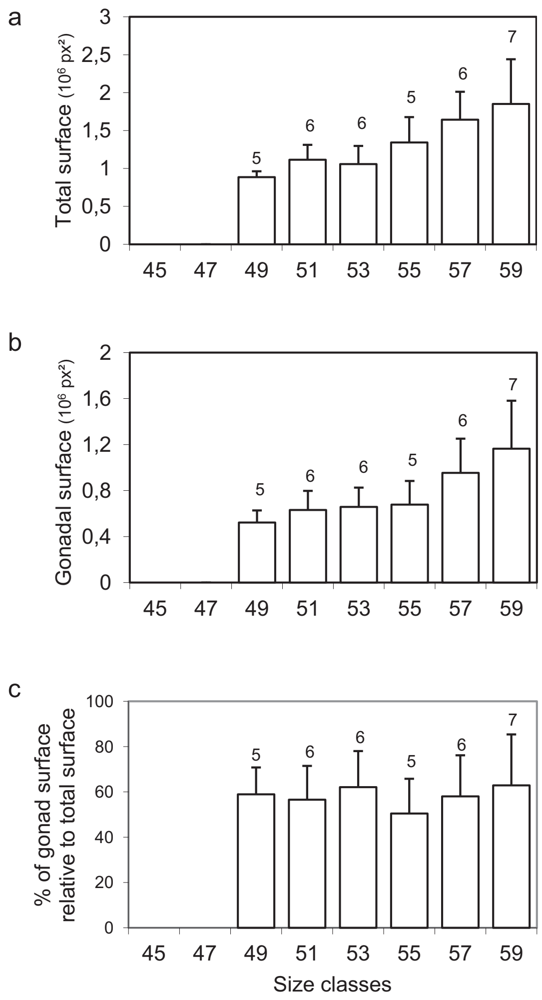

Fig 9. Measurement of tissue surfaces for mature females expressed in pixel^2 (px^2); a: total surface; b: gonadal surface; c: ratio of gonad surface to total surface. Bars correspond to standard deviations. The number of mature females is given over bars for each date.

in order to return the animals under the MLS to the fishing area. Whelk fishing has also been closed in January since 2009. However, it has become obvious that the management of whelk fishing needs to consider not only size distribution data but also local physiological parameters. The latter criteria include the size and age at which whelks become sexually mature. For *Buccinum*, these data may fluctuate greatly according to location, especially as sexual maturation is directly related to environmental parameters like temperature (Shelmerdine et al. 2007). In this study, we demonstrated that local characteristics of whelk biology such as growth and reproduction are highly relevant and useful for fisheries management. In order to provide a more accurate assessment of biological parameters, we sampled animals every two months over a whole year. Our investigations were performed on whelk samples over 45 mm length obtained by fishing with pots. However, this sampling method only provides information about the harvested animals, which might not be perfectly representative of the entire whelk population. For this reason, the size distribution parameters should be considered with caution because the mode of fishing (and sampling) is based on food palatability and animal motility. Despite these limitations, our study of whelk reproduction should still be representative because small whelks under 45 mm were demonstrated not to develop mature gonads, and large animals over 61 mm represented only 6 to 7% of the total population caught in 2008.

The relationship between length and weight for *Buccinum undatum* meant that the relative growth rate could be calculated. Its value (b = 2.955) confirmed that growth in terms of shell length is greater to body weight increase, as found in other gastropods including *Buccinum* species (Ilano et al. 2004 for *Buccinum isaotakii*, Narvarte 2006 for *Buccinum globulosum*, Santarelli and Gros 1985 for *Buccinum undatum*). Our results are in line with data previously gathered in the same geographical area (Santarelli and Gros 1985). Accordingly, the weight to size relationship was similar between the present study and that conducted in 1985 ($a = 9.42 \times 10^{-5}$, $b = 3.05$).

Operculum striae were used to estimate the age of *Buccinum undatum*. We observed a great variation between the lengths of whelks showing the same number of striae. However, the mean number of striae was found to increase progressively for increasing size classes, with reasonable confidence intervals, leading to validation of this age reading strategy. The relationships age-length and age-weight were also clarified. The data revealed a rather good fit with the von Bertalanffy growth curves, although the calculated L_∞ value (73 mm) was probably underestimated due to the restricted sampling. Despite the fact that whelks over 70 mm length were very scarce in this fishing area, specimens reaching 78 mm could sometimes be observed. In *B. undatum*, L_∞ values vary from 66 mm in southern England (Shelmerdine et al. 2007) to 108 mm in France (Santarelli-Chaurand 1985) indicating that growth parameters may differ between relatively close areas, possibly in relation with water temperature or trophic conditions.

The determination of sexual stages is currently based on different approaches. Thus, a visual observation of gonad and accessory glands can establish a gonadal index. Alternative validated methods are: dissection and weighing of gonads and/or accessory glands, measurement of penis size relative to shell length for males or the use of biopsies (Valentinsson et al. 1999; Valentinsson 2002; Brokordt et al. 2003; Henderson and Simpson 2006). These methods are relatively fast and well adapted for regular management of stock sustainability; however, they are not as reliable as histological observations for a precise description of the course of gametogenesis. Histological analysis had already been used for the Buccinidae by Martel et al. (1986) and Averbuj et al. (2010). We chose this histological approach for several reasons. First of all, the technique allows an accurate qualitative analysis of gametogenesis but also a quantitative approach to reproductive investment using image analysis software. Moreover, the comparison between histological and phenotypic sexes (presence or absence of a penis) can identify cases of imposex, frequently described for this species

(Cadée et al. 1995; Evans and Nicholson 2000; Viglino et al. 2006). During our study over a whole year ($N = 960$), no cases of imposex were observed. In accordance with gametogenesis description in other molluscs, four histological stages were determined for each sex. The criteria of gametogenesis stage determination were discriminating enough to unequivocally determine the stages for every sampled animal, including the smaller ones. *B. undatum* exhibits an annual sexual cycle with gametogenesis reinitiation mainly occurring in winter (December and February) when the water temperatures are low (under 10 °C). We observed the progression of gametogenesis during spring and summer, concomitantly with the increase in water temperature, and gonads became mature in October. In 2008, spawning occurred mainly between October and December, consistent with fishermen's observations of fixed eggs on pots. Despite our sampling being restricted to market-sized animals (over 45 mm), the percentage of mature animals clearly depended on animal size. Additionally, L_{50} was different between males and females. Males appeared to reach L_{50} at a smaller size (estimated at 48 mm compared with 52 mm for females) and one year before females. This earlier maturity of males is in accordance with *B. undatum* data obtained in other areas, such as in Canada (Martel et al. 1986) or the Shetland Islands (Henderson and Simpson 2006). Considering that recruitment largely depends on maturity and fecundity of females, this difference between males and females should be taken into account in the improvement of protective measures in a context of fishing activity.

We attempted to evaluate the reproductive investment by measuring both the gonadal thickness and the gonadal surface on the histological section. We confirmed that gonadal thickness increased with maturation from February to October whatever the size classes and the sex of the animals. For this reason, this quantitative value could be considered as a good index of reproductive investment, even though the results could be improved by spacing gonadal sections throughout the whole gonad. The gonadal surface of females was also proportional to their shell size, confirming that animals less than 49 mm in length that reach sexual maturity only produce a few eggs and thus make only a small contribution to the seasonal egg deposition, even though this size group represented more than 23% of the animals fished in 2007 in the study area.

In conclusion, these data confirm the necessity of a strict management of the whelk stock in highly fished areas such as the west coasts of France. This will provide "real time" fishing restriction measures, allowing a sustainable exploitation of the resource. Finally, because water temperature is known to impact the physiology of this species, such investigations may also be of great importance in the context of climatic change.

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