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Variability in the onset of hatching of *Maja brachydactyla* Balss, 1922 (Brachyura: Majidae) in the English Channel in relation to sea temperature

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Summary

Long-term monitoring of zooplankton and temperature has been carried out at the nuclear power station of Flamanville (west coast of Cotentin, English Channel, France) since 1977. Zooplankton sampling and temperature measurements took place at fortnightly intervals, particularly during the spring and summer. In addition, daily records of water temperature were recorded since 1986. The seasonal appearance of *Maja brachydactyla* Balss, 1922 first stage zoeae in the plankton outside the thermal plume near to the power station can greatly vary from year-to-year. Earliest observations have occurred in early June whilst latest observations were made at the end of July. During the period of study, temperature records display a warming trend whilst hatching is gradually recorded earlier in the season. An analysis of year-to-year variability in temperature and hatching date reveals that early hatching is related to higher winter-spring sea temperature. Cumulated temperature (degree-days) has been calculated for different periods (during winter and spring) to detect the time at which temperature may influence the date of initial occurrence of first zoeal stage. There is no relationship with January temperatures whilst a strong correlation is observed for the period ranging from early February to the end of May. Based on regression analysis, a predictive model of timing of zoeae appearance in the plankton is constructed. The model can predict timing of zoeae appearance from mean temperature recorded from February 1st to March10th.

Key words: *Maja brachydactyla*, hatching, larvae, temperature

Introduction

Ecological monitoring has been carried out at Flamanville where is located one of the four nuclear power-stations along the French coast of the English Channel (Fig. 1). From 1977 to 1979 and from 1983 to 1985 zooplankton monitoring has been carried out at monthly or fortnightly intervals during the spring and summer. In 1986, the nuclear power station became operational and the survey focused on two species of crustacean larvae *Homarus gammarus* and *Maja*

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Fig. 1. The western Channel area. Power station sampling sites (stars) and locations mentioned in the text (dots) are indicated. Data for the present study were collected at the site of Flamanville located at the north-western tip of the Cotentin peninsula.

brachydactyla. The spider crab *M. brachydactyla* has a high commercial value and is abundant to the west coast of Cotentin which is known to be the best catching area in France (Kergariou and Véron, 1981). At the sampling site, high numbers of larval stages of this species are sampled (Martin, 2001). The species *M. brachydactyla* Balss, 1922 has recently been identified as a separate species from the Mediterranean (endemic) *M. squinado* Herbst, 1788 (Neumann, 1998). The larval development of *M. brachydactyla* includes two zoeal stages before metamorphosis into a megalopa. The total duration of larval development is only 15–16 days after hatching according to Schlegel (1911). In the bay of Saint-Malo, *M. brachydactyla* larvae are most abundant in waters with depth less than 20 m (Martin, 1985), an observation consistent with the behaviour of mature females which are known to aggregate near the coast in spring for spawning (Kergariou, 1971). After spawning, eggs remain attached to the females pleopods for incubation. The incubation is followed by hatching, when planktonic larvae are released in the water column. Timing of hatching can be deduced from the observation of occurrence of first zoeal stage in the plankton. To the west of Cotentin *M. brachydactyla* first zoeal stages have been observed from August to October (in 1978–79, Martin, 1980) whereas to the south of Brittany (Plogoff) they have been recorded from June to October (in 1979–80, Martin, 1983), indicating strong spatial variability in date of first occurrence. Observations made off the west coast of Cotentin from 1983 to 1992 have showed that the first zoeal stage of *M. brachydactyla* could appear in the plankton as early as mid June (Martin, 1993), indicating that in this area inter-annual variability in the timing of hatching do occur.

The aim of the present study is to describe the phenology of *M. brachydactyla* to the west coast of Cotentin (English Channel), using climate (temperature) and biological (time of hatching) data collected at the Flamanville sampling site from 1986 to present, i.e., during 20 years.

Materials and Methods

Plankton sampling

From 1986 to the present, zooplankton has been sampled every two weeks from the beginning of June to the end of August. The interval between two sampling cruises has sometimes been greater than 15 days owing to bad weather conditions. The sampling station is located 3 miles from the coast at a depth of 25 m and outside the thermal plume of the power station.

Sampling was carried out using a Bongo net, as described by Jossi et al. (1975) fitted with two cylindroconical nets (0.61 m opening, 3 m length) of 500 µm mesh size and a collector which prevents plankton from being damaged. Oblique tows were performed at a speed of around 2 knots from bottom to surface. For each of the two replicates the volume of water sampled varied between 100 and 600 m^3 and was measured with a flowmeter (model 2030 R by General Oceanic).

Samples were preserved using the preservative solution described in Mastail and Battaglia (1978) modified by Bigot (1979); sample jars were maintained in a cool place so that larval pigmentation was kept, in order to facilitate sorting and identification.

Zoeal stages of spider crabs are easily identified by the short dorsal spine associated with the U-shaped cleft on the posterior margin of the telson (Martin, 2001); the megalopa is characterized by protuberances on the carapace dorsal surface associated with the antero-lateral margin forming a right angle. Each sample is fully examined under a binocular microscope. Dates of appearance of first zoeae in the plankton are given in Julian days.

Temperature measurements

From 1986 to present, daily water temperature has been measured at the intake of the power station cooling system. At this location water temperature is on average 0.6°C (± 0.7°C) higher than bottom sea temperature measured at the plankton sampling point located 3 miles from the coast at 25 m depth.

Data processing

Monthly temperature anomalies where calculated for each month of the series as follows:

$$a_{m,y} = t_{m,y} - t_{m.}$$

where $a_{m,y}$ is the anomaly for a given month m and a given year y, $t_{m,y}$ is the original temperature record for the same month and year, and $t_{m.}$ is the temperature for month m averaged over all years. The persistence of anomalies was derived from correlation measurements between interannual time-series of temperature anomalies in a given month (e.g. January) and time-series of temperature anomalies for the following months (e.g. February, March, and so on). Long-term trend in temperature anomalies was tested by correlation analysis (temperature anomalies versus years).

To detect the period during which temperature may affect the date of appearance of first zoeae we have tested the relationship for different periods, from the beginning of the year to the end of May (i.e. before the earliest young zoeae occurred in plankton). The entire period has been divided into 10 day, 20 day and 30 day intervals and the cumulated temperature (degree-days) has been calculated for each interval, each year. In order to avoid inflated correlation coefficients due to serial autocorrelation and to remove trends in the data series, we have transformed the data using first-order differencing (Thompson and Page, 1989) prior to correlation analysis. Synchrony between year-to-year fluctuations in temperature and in timing of hatching where tested using Pearson correlation coefficients between time-series of first-order differenced data.

On the basis of the results provided by the correlation analysis, linear regression models were built to predict the timing of hatching from temperature records. A series of models was constructed using cumulated temperature over increasing duration in order to evaluate model predictability as a function of the seasonal timing of the predictions.

Results

Temperature

Temperature anomalies recorded in January do not tend to persist over the following months, at least not beyond February (Table 1). On the other hand, anomalies recorded in February persist for several months and correlations are still significant ($P < 0.01$) in May or even June ($P < 0.05$). This reveals that year-to-year variations in temperature are coherent throughout the period from February to May, but that anomalies recorded earlier (January) follow a separate dynamics.

A warming trend in temperature is apparent over the period 1986-2005 (Fig. 2) with a significant correlation between years and temperature anomalies over the 4-month period February to May ($r = 0.567$, $P < 0.01$). The warming trend accounts for 32% of the variance in the temperature series. The coldest year on record is 1986 and the warmest is 2002 (Fig. 2).

Timing of hatching

Seasonal variations of water temperature for years

Table 1. Cross-correlation between monthly anomalies of temperature over the period 1986–2005. Dark grey: $P<0.01$, light grey: $P<0.05$, white: not significant

r	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan		0.50	0.17	0.00	0.18	0.39	-0.20	-0.38	-0.57	-0.46	-0.63	-0.59
Feb			0.62	0.70	0.71	0.52	0.16	0.16	-0.04	-0.11	-0.14	-0.23
Mar				0.72	0.79	0.58	0.47	0.38	0.04	0.22	0.18	0.33
Apr					0.89	0.60	0.57	0.52	0.30	0.33	0.36	0.20
May						0.79	0.63	0.53	0.07	0.11	0.20	0.16

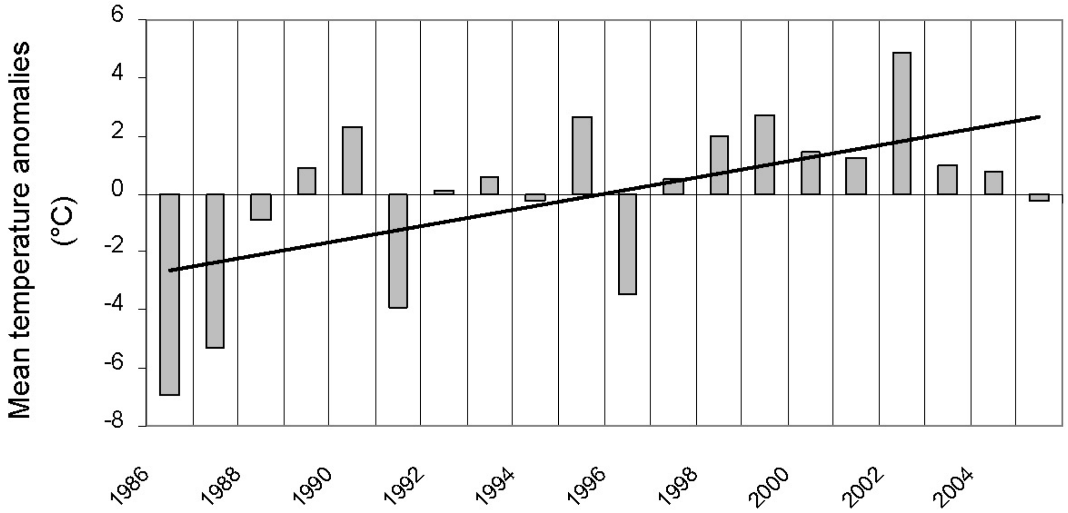

Fig. 2. Year-to-year variations in mean temperature anomalies (°C) during the months February to May for the period 1986–2005. Anomalies are calculated as deviation from the mean temperature over the 20-year period.

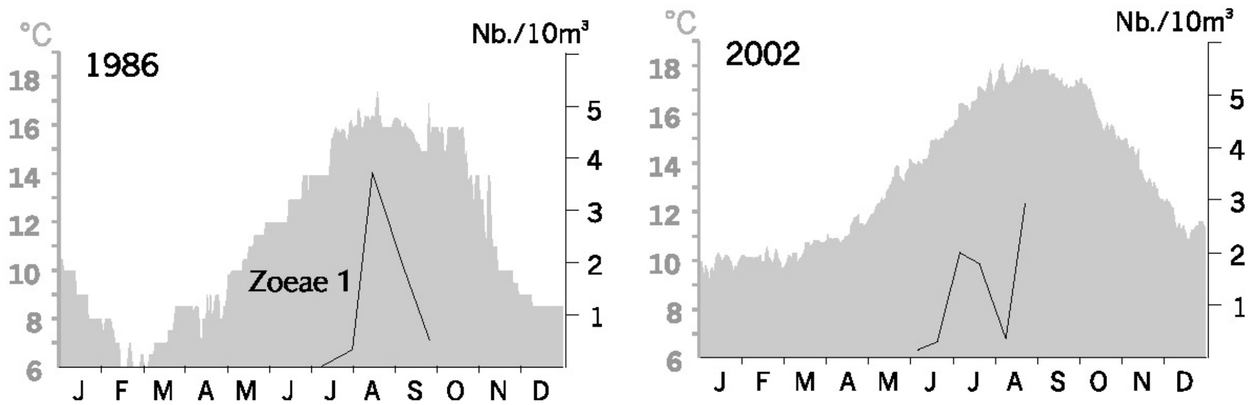

Fig. 3. Seasonal variations in abundance of first zoeal stage of *Maja brachydactyla* (numbers per 10 m^3, black lines) and daily water temperature (°C, grey bars) during 1986 (left) and 2002 (right).

1986 when winter-spring temperatures were the coldest of the series and 2002, the warmest year for this period are shown in Fig. 3. In 1986, the first zoeae appeared at the end of July whereas in 2002, they were observed from early June. Intuitively, hatching period of zoeae seems to be related with winter–spring water temperature.

Table 2. Correlation between first order differenced time-series of cumulative temperature (Degree-days) over different time periods and the onset of hatching (in Julian days). Dark grey: *P*<0.001, medium-dark grey: *P*<0.01, medium-light grey: *P*<0.05, white: not significant

Correlation coefficient (r) *	January			February			March			April			May		
Period beginning on	1st	11th	21st	1st	11th	21st	1st	11th	21st	1st	11th	21st	1st	11th	21st
10 days period	0,10	0,19	0,36	0,61	0,80	0,86	0,52	0,67	0,57	0,85	0,76	0,72	0,73	0,83	0,79
20 days period		0,28		0,76		0,75		0,65		0,84		0,75		0,83	
	0,05		0,50		0,86		0,61		0,75		0,81		0,79		
30 days period	0,16			0,82			0,64			0,86			0,82		
		0,40			0,83			0,75			0,80				
			0,67			0,72			0,79			0,79			

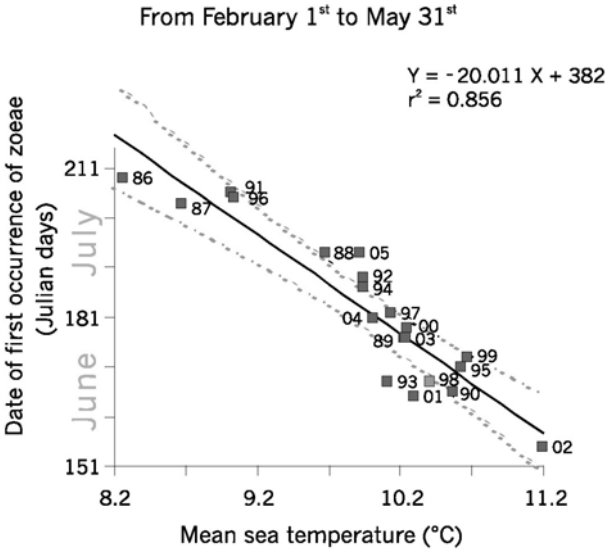

Fig. 4. Date of first observation of zoeae as a function of sea temperature for the period February 1st to May 31st. Linear regression model (black line) and confidence interval at 1% level (dotted lines) are indicated.

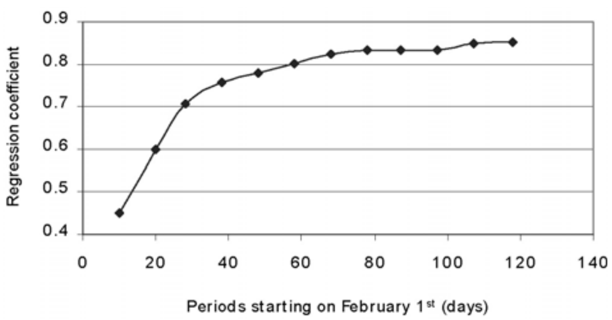

Fig. 5. Percentage of variance in timing of zoeae appearance explained by linear regression models as a function of the length of the period during which temperature measurements are considered.

The correlation analysis between time-series of cumulated temperatures and timing of hatching (Table 2) shows that there is no significant correlation

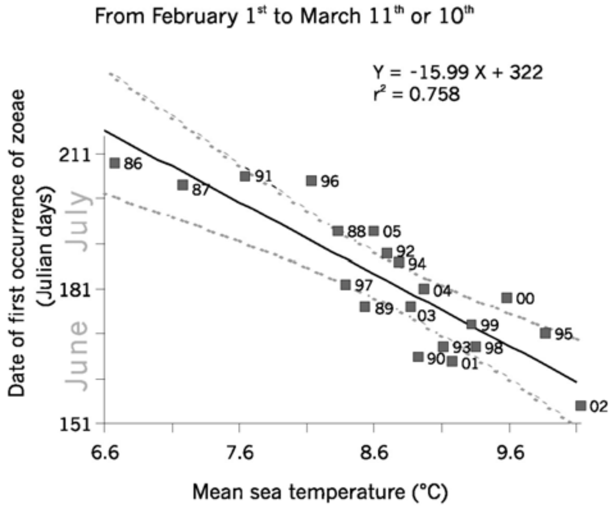

Fig. 6. Date of first observation of zoeae as a function of sea temperature for the period February 1st to March 10th. Linear regression model (black line) and confidence interval at 1% level (dotted lines) are indicated.

between January temperature and the first occurrence of zoeae whereas the correlation is significant from February to the end of May, with a slight decrease around early March.

On the basis of these results, it is possible to construct a linear prediction model of the first occurrence of zoeae from mean water temperature measured from early February to the end of May (Fig. 4). The model shows that an increase in 1°C is associated with a 20 days advance in the timing of hatching. Variations in temperature anomalies between 1986 and 2002 have reached 3°C leading to a 2 months shift in the onset of hatching. The fraction of variance explained by the model reaches 85% which suggests that temperature may be the main driver determining year-to-year variations in the timing of hatching.

Since temperature anomalies in February are related to those of the following months (Table 1), it is likely that accurate predictions of timing of hatching can be produced early in the season, i.e. before temperature records are available for the whole February–May period. The fraction of variance explained by linear regression models increases as more temperature data is available (Fig. 5), reaching a maximum when the entire season is considered. Although early predictions based on a short temperature record (one or two weeks) explain less than 50% of the variance, by the 10th March, a simple linear model can already account for 75% of the observed variability in timing of hatching (Figs. 5 and 6). Fig. 6 shows that the two months shift in timing of zoeae appearance can be explained by the 3.5°C temperature range observed for the period from February 1st to March 10th.

Discussion

The multi-decadal temperature increase recorded at the Flamanville site is consistent with global and regional temperature trends established by the International Panel on Climate Change (IPCC, 2001) which indicates that greatest recent temperature increase is observed in the European region. This observation also confirms the warming trend over the French North Sea coast described in Woehrling et al. (2005).

The precision and accuracy of the determination of timing of first zoeal occurrence depends on the starting date of sampling each year as well as on the frequency of sampling during the season. In 1989 the first observation was made on July 11th coinciding with the peak of zoeal abundance and was therefore probably too late in the season to detect the first appearance of zoeae. As a consequence we considered that the first zoeal stage appeared 15 days before. In 2005, owing to bad weather conditions, there was no sampling between 14th June and 12th July and zoeae were first observed on the latter date. However, predicted date of first observation provided by the regression model is the 3rd of July. The lack of observation may therefore have been critical for the precise determination of the timing of zoeae first appearance and late timing in 2005 (Fig. 4) is likely artefactual.

Hatching is preceded by three important biological processes: gonad maturation, spawning and incubation (whilst the eggs remain attached to the setae on the endopodites of female pleopods). Assuming that these three processes can be influenced by temperature, the lack of correlation between January sea temperature and timing of hatching suggest that none of these processes have started in January. On the other hand, the significant correlation between February sea temperature and timing of hatching suggests that at least one of these three processes is already at play in February.

Although gonad maturation of *M. brachydactyla* may be influenced by temperature as García-Flórez and Fernández-Rueda (2000) suggest in their discussion, this has not yet been established and the details of the gonad maturation process has not been studied in the area of Cotentin.

Spawning time can be deduced by observations of egg-bearing females. Earlier reports show that the timing of the breeding period of *M. brachydactyla* females in the northeast Atlantic varies. Breeding starts in December off the coast of Asturias (northwest Spain, García-Flórez and Fernández-Rueda, 2000), in January in the Arosa Estuary (Galicia, Spain, González-Gurriarán et al., 1993) or in March in west Ireland (Brosnan, 1981). According to Kergariou (1975) egg-bearing females can be found from February to October along the French coast of the English Channel and Atlantic. However Kergariou does not report the precise location of sampling and the length of the breeding season may vary along the coast. According to Le Foll (1993), the west part of the English Channel can be divided in two areas: the area around Morlaix (and Brest) where the breeding season (egg-bearing females) starts in February and the area of Paimpol and Saint-Malo where breeding takes place in April or May. Observations of spider crab larvae in the plankton collected at Plogoff show a similar shift in the date of onset of hatching when compared with observations performed at Flamanville (Martin, 1983). As winter–spring variations in sea temperature at Plogoff during 1979–80 are similar to those observed at Flamanville during the warmest year (2002, minimum about 9°C and 10–11°C in April), this shift in timing of hatching can be attributed to differences in mean sea temperature between the two areas.

Laboratory studies have shown that the duration of egg incubation is related to temperature (Kergariou, 1975; González-Gurriaran et al., 1998; García-Flórez and Fernández-Rueda, 2000). Observations of egg-bearing females from mid-May in Les Minquiers (an area situated 9 miles south of Jersey), in 1986 (Le Foll, 1993) and observations of zoeae at Flamanville in the same year from the present study suggest that duration of incubation is greater than 2 months when mean temperature is of 13.8°C over the period. This is consistent with incubation duration observed from laboratory experiments by Kergariou (74 days at a mean temperature of 14°C, 1975).

Thus, during cold years (such as 1986) observations made to the west coast of Cotentin suggest that first ovigerous females observed from mid May (Le Foll) hatch their eggs at the end of July (our observations of zoeae), whilst during warm years (such as 2002) the onset of hatching can be at least as early as the beginning of June. The exact timing of spawning in warm years is still unknown, but it is possible that spawning could occur as early as February in the west coast of Cotentin when temperature are around 10°C. Additional observations are needed to confirm this hypothesis.

The influence of climate variability, and in particular of fluctuations in temperature, has been shown to influence the phenology of terrestrial birds (Crick et al., 1997, McCleery et al., 1998) and oceanic plankton (Edwards and Richardson, 2004) or other animal and plant groups (Wuethrich, 2000). The present study provides additional evidence that the phenology of coastal marine invertebrates can respond rapidly to fluctuations in local temperature that are related to large-scale climate. Expected future warming during winter and spring, as predicted by the International Panel on Climate Change (IPCC, 2001), may result in earlier hatching of spider crab larvae in the western English Channel.

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