


The biology and ecology of *Necrodes littoralis*, a species of forensic interest in Europe

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Abstract *Necrodes littoralis* (Linnaeus, 1758) (Coleoptera: Silphidae), also known as the “shore sexton beetle,” is a common silphid beetle that visits and breeds on large vertebrate cadavers. This study describes, for the first time, the involvement of *N. littoralis* on human corpses based on a large dataset of 154 French forensic cases. Various parameters regarding corpse location, decomposition stages, and entomofauna were extracted from each file. Compared to all of the forensic entomology cases analyzed between 1990 and 2013 (1028), *N. littoralis* was observed, on average, in one case out of eight; most of these cases occurred during spring and summer (73.5 %). More than 90 % of the cases were located outdoors, especially in woodlands, bushes, and fields. The decomposition stage of the corpse varied among cases, with more than 50 % in the advanced decomposition stage, 36 % in the early decomposition stage, and less than 10 % in the fresh, mummified, or skeletonized stages. Regarding other necrophagous species sampled with *N. littoralis*, Calliphoridae flies were found in 94 % of the cases and Fanniidae/Muscidae in 65 % of the cases. *Chrysomya albiceps*, a heliophilic species mostly located in the Mediterranean area, was present in 34 % of the cases (only 20 % in the whole dataset). The most common coleopteran species were *Necrobia* spp. (Coleoptera: Cleridae) and *Creophilus maxillosus* (Coleoptera: Staphylinidae); these beetles were observed in 27 % of the

cases. The over-representation of these species is likely due to similar requirements regarding the climate and decomposition stage. As *N. littoralis* is frequently observed and tends to become more common, we conclude that the developmental data for this species would be a precious tool for forensic entomologists in Europe.

Keywords Silphids · Outdoor corpses · Colonization · Taphonomy · PMI estimation

Introduction

Necrodes littoralis (Linnaeus, 1758) (Coleoptera: Silphidae), also known as the “shore sexton beetle,” is a common silphid beetle that visits and breeds on large vertebrate cadavers. This insect is both a necrophage and a predator of fly larvae (maggots) and is thus a species of interest for forensic entomology [1]. Although many authors reported *Necrodes* species on human corpses, only a few studies mentioning their biology can be found in the literature [1–12]. This study describes, for the first time, the involvement of *N. littoralis* on human corpses based on a large dataset of 154 French forensic cases.

N. littoralis is a large (15 to 25 mm long) necrophagous beetle. The adults are shiny black, with a characteristic bump about three quarters of the way down the tricolored truncated elytra. Larvae are campodeiform, with a central longitudinal light-colored line running the entire length of dorsum. Details on the morphology of a similar species, *Necrodes surinamensis*, can be found in the extensive study by Ratcliffe [12]. Adults can be observed on carrion, where they feed and breed, providing the hatched larvae with an instant supply of food. Like many other necrophagous species, they are attracted to carcasses by volatile organic compounds (VOCs) produced in the decomposition process [13–15]. They

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colonize carcasses late in decomposition, and a long interval preceding their appearance on a cadaver is generally observed: Matuszewski et al. demonstrated from field data that the *N. littoralis* pre-appearance interval was strongly correlated to the preceding ambient temperature and can be estimated from meteorological data [5, 7]. Once on a cadaver, adults mostly feed on Diptera larvae but can also consume decaying tissues [12]. After mating, females start to oviposit in the soil near and under the carrion. The number of eggs per female can exceed 25 (personal observation), but Ratcliffe reported that *N. surinamensis* females oviposited during most of the time they were observed on the cadavers. The larvae feed actively on decaying material and can also predate Diptera larvae [16]. Frączak and Matuszewski recently provided useful data for larval instar determination [1]. Pupation occurs in pupal cells dug into the ground away from the cadaver. As for many insects, the developmental time strongly depends on the temperature [12]. Surprisingly, no developmental data have been published to date for *N. littoralis*, but some indicative values can be found in Ratcliffe (1972) for *N. surinamensis*.

In a forensic context, several authors reported *N. littoralis* from pig decomposition studies [2–5, 7, 17–19], but we found only a few reports of this species on human corpses. Easton and Smith found 13 *N. littoralis* beetles on a 17-day-old cadaver in October 1969 [20]. Easton noted that “*Necrodes littoralis* used to be taken much more commonly than of recent years,” but did not provide any data or references to support his assertion. The authors also hypothesized that *N. littoralis* were attracted by maggots rather than the cadaver. In their extensive study on the work of Dr. M. Leclercq, a forensic pathologist who developed forensic entomology in Belgium during 36 years, Dekeirsschieter et al. reported ten forensic cases (out of 132) involving *N. littoralis*. However, in no case this species was extensively described nor used for PMI estimations [21].

To fill these knowledge gaps regarding the biology of *N. littoralis*, we report here the habits of this species based on the analysis of 154 forensic cases involving *N. littoralis* adults or larvae sampled on human corpses.

Dataset and methodology

This study is based on the analysis of 1028 forensic entomology cases investigated by the French gendarmerie department (IRCGN) from 1990 to 2013. The data are those provided by law enforcement agencies and the forensic pathologist and entomologist who worked on each of these cases. From this extensive dataset covering the whole metropolitan French territory (Western Europe), 154 cases involving *N. littoralis* were found and investigated. It must be kept in mind that these forensic data only provide a snapshot of the entomofauna and decomposition stages at the time that each corpse was discovered; accordingly, they do not fully reflect the temporality of entomological and decomposition processes. Furthermore, the

forensic evidences of this study were sampled by different people: although they were trained and followed detailed protocols, a sampling effect cannot be excluded.

Various parameters regarding the corpse location, decomposition stage, entomofauna, and presence of *N. littoralis* were extracted from each file. The *N. littoralis* specimens sampled on the corpse were sorted into three developmental categories: larvae, adults, or exuviae/dead adults. The corpse location was described regarding the indoor or outdoor position, geographical location (city), and type of environment (surroundings of the corpse). The other necrophagous species sampled on the corpse were also noted. Six categories were used to describe the decomposition stages: fresh, early decomposition, advanced decomposition, mummification, skeletonization, and other (e.g. burnt corpses). The PMI_{min}, calculated from entomological evidence using different methods and datasets, was not included in the analysis. The maximum post mortem interval (PMI_{max}), defined as the period between when the victim was reported alive for the last time and the corpse was discovered, was known in 54 cases and was analyzed.

Statistical analysis

Statistical analyses were performed using XLSTAT 2011.4.02 software by Addinsoft. All tests were performed under the $\alpha=0.05$ significance threshold. Unilateral *z* test was used to compare the proportion of *N. littoralis* cases involving a given parameter to the reference dataset (e.g., proportion of outdoor *N. littoralis* cases compared to the proportion of outdoor forensic entomology cases). A chi-square goodness-of-fit test was used to compare calendar year distribution between *N. littoralis* cases and reference dataset. Consecutive months with low number of cases (<5) were pooled to meet test assumptions (January+February+March, April+May, and November+December).

Results

Prevalence, location, and seasonality

For more than 20 years, *N. littoralis* was observed in 154 cases that were analyzed in France. Compared to all of the forensic entomology cases analyzed between 1990 and 2013 (1028), the mean prevalence was 14 %. In other words, on average, *N. littoralis* was observed in one case out of eight. This repartition slightly evolved during the last few years: *N. littoralis* became more frequent in forensic entomology samples since 2000 (Fig. 1).

Regarding developmental instars, 80 % of *N. littoralis* cases involved adults, 37.4 % involved larvae, and the presence of both adults and larvae were observed in 24.5 % of cases. Lastly, dead individuals and/or exuviae were sampled in only 17 cases (11 %).

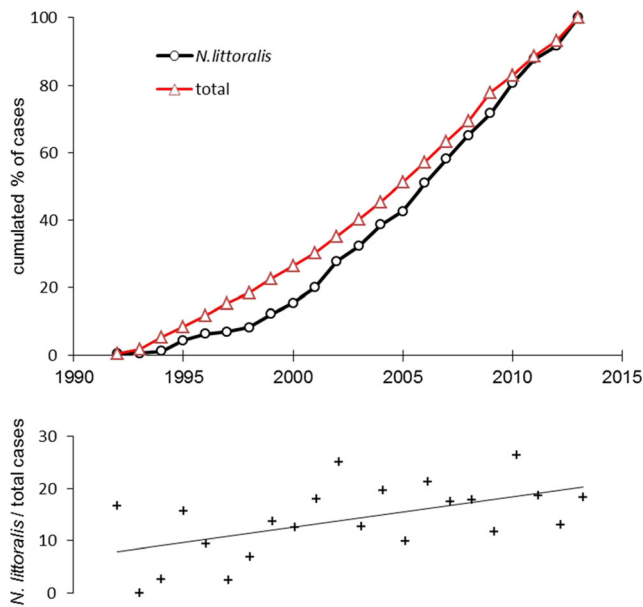


Fig. 1 Evolution of forensic entomology cases over time. Upper part: red triangles represent the whole French forensic entomology cases (total=1028) and blue circles the cases involving *N. littoralis* (total=155). Lower part: percentage of cases involving *N. littoralis* (black crosses) and average trend (linear fitting, $R^2=0.3$)

Among the cases where *N. littoralis* was found, 91.6 % were outdoor cases and 8.4 % were indoor cases. This spatial distribution differed from the one observed for other forensic cases, with significantly more outdoor cases in the *N. littoralis* dataset (unilateral *z* test, $z=9.49$, $p<0.0001$). In outside locations, most cases were located in woodlands, bushes, and fields; only a few were found at the sea side (Table 1). Lastly, *N. littoralis* was under-represented in riverside and dump corpses (unilateral *z* test, Table 1).

Table 1 Repartition of forensic cases with and without *N. littoralis* according to their location

| | <i>N. littoralis</i> | | <i>z</i> score | <i>p</i> value |
|------------------|----------------------|-------------|----------------|-------------------|
| Indoor | 8.4 | 34.2 | -6.41 | <0.0001 |
| Outdoor | 91.6 | 65.8 | 6.41 | <0.0001 |
| Bushes | 25.5 | 26.1 | -0.13 | NS |
| Field | 10.6 | 6.1 | 1.93 | 0.03 |
| Residential area | 8.5 | 5.3 | 1.46 | NS |
| Woodland | 41.8 | 41.3 | 0.13 | NS |
| Riverside | 5.0 | 9.5 | -1.74 | 0.04 |
| Dump | 0 | 4.7 | -2.62 | 0.004 |
| Sea side | 0.7 | 1.1 | -0.41 | NS |
| NA | 7.8 | 5.9 | 0.83 | NS |
| <i>N</i> outdoor | 141 | 640 | | |

Total number of cases with known location: *N. littoralis* dataset=154; total dataset=971. Bold font indicates significant differences between the two observed repartitions (unilateral *z* test). Percentages for outdoor location are reported compared to total outdoor cases

NS not significant, NA detailed location not available

Regarding seasonality, most of the cases occurred during spring and summer, with 13 % of the total cases in June, 24.5 % in July, 16 % in August, and 20 % in September (Fig. 2). These seasonal patterns differed from the distribution of the cases in a calendar year observed for the total dataset (χ^2 test, $\chi^2=18.85$, $p=0.009$). Lastly, we observed that the *N. littoralis* cases covered the whole French territory (Fig. 3). Their distribution in the country appears to be quite uniform and not restricted to a given climatic area, coastal region, or given latitude or longitude gradient. Furthermore, no relevant evolution of the spatial distribution over time was observed from the dataset.

Correlation with decomposition stages

The date on which the victim was seen alive for the last time was known with certainty in 54 cases. Among these cases, the maximum post mortem interval (PMI_{max}, i.e., the number of days between the day on which the victim was seen alive for the last time and the discovery of the cadaver) ranged between 5 days and 22 months (Fig. 4). Among the 154 cases analyzed, more than 50 % of the cadavers in which *N. littoralis* was sampled were in the advanced decomposition stage and 36 % were in early decomposition. Fresh, mummified, and skeletonized corpses accounted for less than 10 % (Table 2 and Fig. 4). The distribution of *N. littoralis* over the decomposition process differed from the global cases distribution, with significantly fewer fresh corpses observed and more corpses in advanced decomposition as well as mummified cadavers (unilateral *z* test, Table 2). The probability to observe a given instar varies with PMI_{max}: adults were observed even in short PMI_{max} cases, closely followed by larvae. The

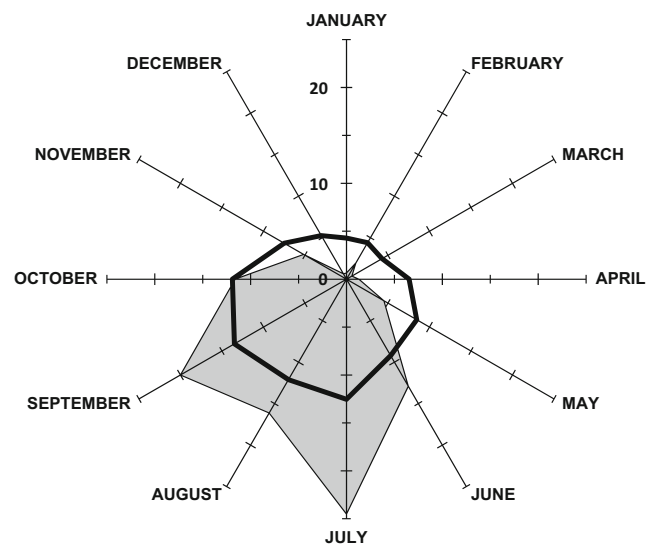
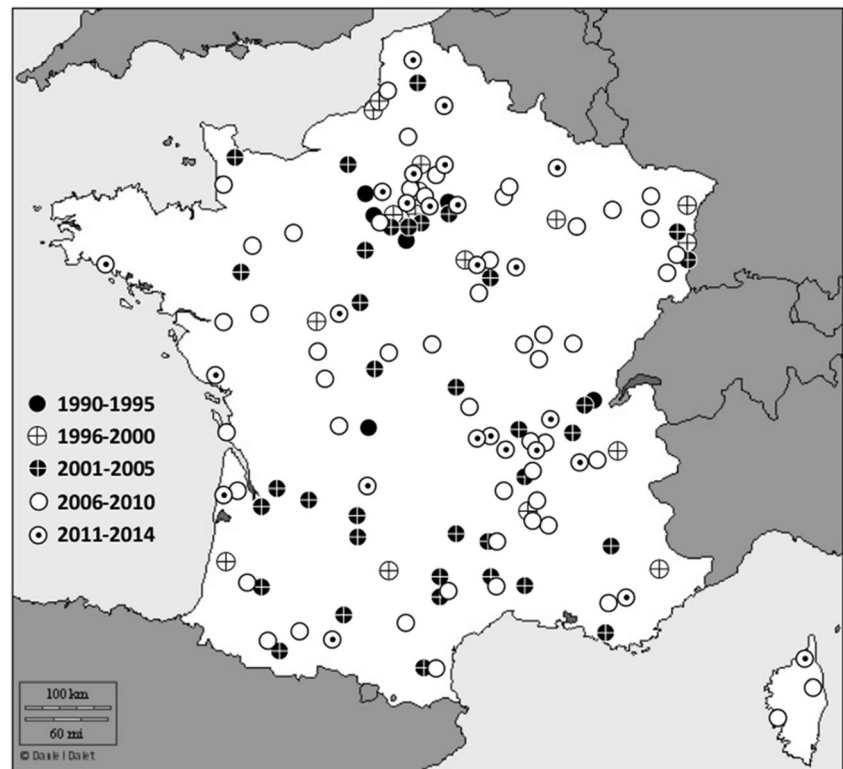


Fig. 2 Seasonal distribution of forensic cases (% of total cases, gray area) involving *N. littoralis* across the year. The distribution of the whole cases dataset is reported with a black line

Fig. 3 Spatial distribution of forensic cases involving *N. littoralis* on the French territory over years



presence of both adults and larvae was observed only when PMI_{max} ranged between 10 and 69 days, while exuviae and/or dead adults were sampled on corpses with a PMI_{max} longer than 650 days (Fig. 4).

Associations with other species of forensic interest

Among the dipterans sampled together with *N. littoralis*, calliphorid flies were found in 94 % of the cases and Fanniidae/Muscidae in 65 % of the cases (Fig. 5 and Table 3). *Calliphora vomitoria* was the leading species (one case out of two), while *Ophyra* sp. was found in 37 % of the cases. *Chrysomya albiceps*, a heliophilic species mostly located in the Mediterranean area, was present in 34 % of the cases

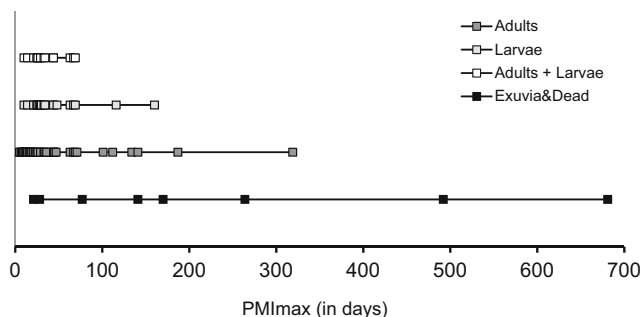


Fig. 4 Distribution of *N. littoralis* developmental instars according to the PMI_{max} (i.e., the number of days between the day on which the victim was seen alive for the last time and the discovery of the cadaver)

(only 20 % in the whole dataset). The most common coleopteran species associated with *N. littoralis* were *Necrobia* spp. (Coleoptera: Cleridae) and *Creophilus maxillosus* (Coleoptera: Staphylinidae); these beetles were observed in 27 % of the cases. With a total of 35 cases out of 154 (22.6 %), clown beetles *Saprinus* spp. (Coleoptera: Histeridae) were also frequent, closely followed by larder beetles (Coleoptera: Dermestidae), observed in 32 cases. Lastly, common dung beetles (*Geotrupes* spp., Coleoptera: Geotrupidae) were found in 9 % of cases. Most of these necrophagous or saprophagous beetles were over-represented in *N. littoralis* cases compared to the reference dataset (Table 3, unilateral z test).

Discussion

This study was designed to infer the habits and preferences of *N. littoralis*, a necrophagous beetle, from an extensive dataset of more than 1000 forensic entomology cases that occurred in France between 1990 and 2013. In total, 154 cases involving *N. littoralis* were found and analyzed according to three main axes: post mortem interval and decomposition stages; prevalence, location, and seasonality; and associations with other insects of forensic interest.

Note that this study is based on the material that was sampled when the corpses were discovered. As human corpses are inherently not homogeneously or randomly distributed over space and time, they constitute a biased dataset. Accordingly,

Table 2 Repartition of forensic cases with and without *N. littoralis* according to the decomposition stage of the cadaver (% of total cases)

| | <i>Necrodes littoralis</i> | Total cases | z score | p value |
|-------------------------------|----------------------------|-------------|-------------|-------------------|
| Fresh | 0.6 | 9.2 | -3.6 | 0.00015 |
| Early decomposition | 36.4 | 37.7 | -0.3 | NS |
| Advanced decomposition | 52.6 | 31.3 | 5.2 | <0.0001 |
| Mummification | 0 | 3.6 | -2.4 | 0.009 |
| Skeletonization | 9.1 | 9.6 | -0.2 | NS |
| Burnt | 0.0 | 1.9 | -1.7 | 0.04 |
| Other | 1.3 | 6.9 | | |

Total number of cases with known decomposition stages: *N. littoralis* dataset=154; total dataset=1014. Bold font indicates significant differences between the two observed repartition (unilateral z test)

NS not significant

there are several known limitations to the results. Despite the training of the crime scene technicians, sampling bias cannot be excluded. Lastly, insect samples do not reflect the whole decomposition process that occurred before corpse discovery. These biases are discussed in the following section and should be kept in mind while attempting to extrapolate conclusions to forensic cases.

Prevalence, location, and seasonality

N. littoralis appears as an uncommon species, occurring in only 14 % of French forensic entomology cases. This value is consistent with previous observation: according to the synthesis published by Dekeirsschieter et al., *N. littoralis* was present in 7.5 % of the 132 Belgian cases analyzed by Dr. M. Leclercq from the 1970s to 2005 [21]. Due to the large size and high mobility of this insect, a lack of detection and subsequent lack of sampling can be a priori excluded. A more likely explanation could be the selectivity and seasonality of this species. Preferences for (1) outdoor location and (2) decomposed cadavers likely contribute to the infrequent colonization of human cadavers, which are often located indoors and discovered during early decomposition stages. Indeed, while outdoor corpses account only for two thirds of the forensic entomology cases, they account for more than 90 % of *N. littoralis* reports. Dekeirsschieter reported the same trend from Dr. M. Leclercq's dataset: most cases involving *N. littoralis* were located outdoors, especially in forest or rural area [21]. Despite some incidental observations of huge *N. littoralis* colonization inside houses or apartments, the actual ability of this large beetle to detect small openings, to fly and land with accuracy, and to crawl inside buildings is uncertain. Accordingly, the difficulty for this species to access concealed corpses may explain the lack of *N. littoralis* on certain indoor corpses. Furthermore, due to the rapid discovery of indoor cadavers (e.g., by neighbors), the average PMI of indoor cases may be too short to attract *N. littoralis*.

Regarding the spatial distribution of *N. littoralis* forensic records, the wide distribution of this species in the French

territory was noted. *N. littoralis* is also known as the shore sexton beetle: from its Latin and vernacular names, one may think this species would be preferentially found close to shore. The present study does not support this idea; *N. littoralis* was found throughout the whole territory and was not restricted to the coastal areas. Such a diversity of habitat was also observed on a larger scale; according to the United Nations Environment Program/Global Resource Information Database (UNEP/GRID), *N. littoralis* was reported in most European countries [22]. Its distribution includes Austria, Hungary, Slovakia, and the Czech Republic, which are far from the sea. Detailed *N. littoralis* distribution maps are also available online for Great Britain and Ireland: many observations are reported in coastal areas, but many others are located in the back country [23]. From these data and our forensic cases dataset, it is obvious that *N. littoralis* is not only a littoral species.

Most of the cases involving *N. littoralis* were located outdoors and occurred in woodlands, bushes, or fields; only a few were found on the riverside or at the seashore. During the preparation of this study, many field and forensic entomologists reported to us that they found this species mainly on large mammalian cadavers in woodland areas (personal communication). This trend was also confirmed by the literature: in its extensive study on insect succession and carrion decomposition in Poland, Matuszewski found *N. littoralis* in abundance in various forest habitats [2, 18, 19, 24]. According to these observations and our dataset, *N. littoralis* appears as a rural species mainly found in forest areas or fields, but also in bushes or residential areas in cities.

We also observed a strong seasonality in cases involving *N. littoralis*, with 83 % occurring during spring and summer, i.e., the dry and hot season (Fig. 3). Seasonality in silphid beetles was previously noted by Lingafelter, who observed a bimodal peak of activity for *N. surinamensis* in Kansas [25]. This seasonal distribution was not supported by Ratcliffe, who assumed that overlapping generations should occur as long as conditions are favorable. This assumption seems not to be true regarding *N. littoralis* forensic cases in France. The species was observed from May to November, with the most cases in

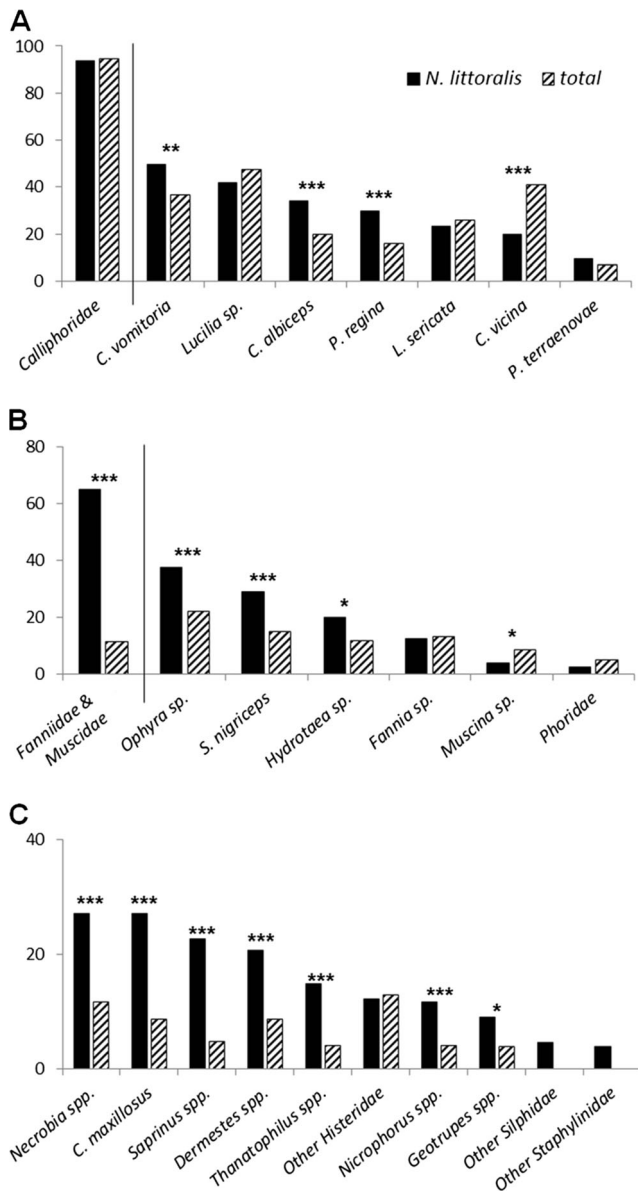


Fig. 5 Occurrence of main insect species of forensic interest sampled with *N. littoralis* (% of total cases). **a** Diptera Calliphoridae; **b** other Diptera; **c** Coleoptera. Histograms in *black* are for the *N. littoralis* dataset and *shaded* ones for the whole forensic cases dataset. Total number of cases with known species (reference dataset)=1028, total number of cases with *N. littoralis*=154. Significant differences compared to the reference dataset (unilateral z test) are reported as follows (unilateral z test): * $p < 0.05$, ** $p \leq 0.001$, *** $p < 0.0001$

July, August, and September. This trend is also consistent with the dataset of Dr. M. Leclercq, who mostly observed *N. littoralis* in Belgium during spring and summer [21]. Because this distribution clearly differed from the distribution of other forensic entomology cases, this seasonality indicates the ecological and thermal preferences of the species. We thus concluded that *N. littoralis* likely has strict thermal exigencies and avoids cold and rainy/humid months. However, the spatial distribution of the species in France was not restricted to the

Table 3 Association to other species reported as the % of *N. littoralis* cases involving these taxa. Total number of cases with known species (reference dataset)=1028, total number of cases with *N. littoralis*=154. Significant differences compared to the reference dataset are reported in bold (unilateral z test). NS: not significant.

| | <i>N. littoralis</i> | total | z score | p-value |
|----------------------------------|----------------------|-------------|--------------|-------------------|
| <i>Calliphoridae</i> | 93.5 | 94.7 | -0.25 | NS |
| <i>C. vomitoria</i> | 49.7 | 36.9 | 3.12 | 0.001 |
| <i>Lucilia</i> sp. | 41.9 | 47.4 | -1.22 | NS |
| <i>C. albiceps</i> | 34.2 | 20.1 | 3.99 | <0.0001 |
| <i>P. regina</i> | 29.7 | 16.1 | 4.17 | <0.0001 |
| <i>L. sericata</i> | 23.2 | 26.1 | -0.73 | NS |
| <i>C. vicina</i> | 20 | 41 | -4.96 | <0.0001 |
| <i>P. terraenovae</i> | 9.7 | 6.8 | 1.31 | NS |
| Fanniidae/Muscidae | 65.2 | 11.6 | 16 | <0.0001 |
| <i>Ophyra</i> sp. | 37.4 | 22.3 | 4.15 | <0.0001 |
| <i>S. nigriceps</i> | 29 | 15.2 | 4.28 | <0.0001 |
| <i>Hydrotaea</i> sp. | 20 | 12 | 2.77 | 0.0028 |
| <i>Fannia</i> sp. | 12.3 | 13.4 | -0.4 | NS |
| <i>Muscina</i> sp. | 3.9 | 8.8 | -2.07 | 0.019 |
| <i>Phoridae</i> | 2.6 | 4.9 | -1.3 | NS |
| <i>Necrobia</i> spp. | 27.1 | 11.7 | 5.16 | <0.0001 |
| <i>C. maxillosus</i> | 27.1 | 8.8 | 6.76 | <0.0001 |
| <i>Saprinus</i> spp. | 22.6 | 4.8 | 7.96 | <0.0001 |
| <i>Dermestes</i> spp. | 20.6 | 8.7 | 4.59 | <0.0001 |
| <i>Thanatophilus</i> spp. | 14.8 | 4 | 5.57 | <0.0001 |
| <i>Other Histeridae</i> | 12.3 | 13 | -0.27 | NS |
| <i>Nicrophorus</i> spp. | 11.6 | 4.1 | 3.89 | <0.0001 |
| <i>Geotrupes</i> spp. | 9 | 3.9 | 2.78 | 0.003 |
| <i>Other Silphidae</i> | 4.5 | NA | | |
| <i>Other Staphylinidae</i> | 3.9 | NA | | |

Total number of cases with known species (reference dataset)=1028, total number of cases with *N. littoralis*=154. Significant differences compared to the reference dataset are reported in bold (unilateral z test) NS not significant

warmer part of the country and covered the whole French territory. Such a wide distribution was also observed by Ratcliffe in *N. surinamensis*. This species was mostly reported in the eastern half of the United States, but also in the north-western quarter of the country and up to Canada and South America. As a widespread species, Ratcliffe also pointed out the wide variety of climates experienced by *N. surinamensis*.

Interestingly, the distribution of cases involving *N. littoralis* over the last 20 years showed a slight increase. Since 2000, the number of *N. littoralis* cases increases more rapidly than the overall number of cases (Fig. 1). Due to the large size of this beetle, this trend is unlikely due to better sampling by law enforcement personnel. The spatial distribution of the cases over time did not show a clear expansion into new geographic areas and do not support the hypothesis of a spreading of this

species (Fig. 3). It could more likely be due to some very hot years, resulting in an increase of both advanced decay stages and period of *N. littoralis* activity.

Correlation with decomposition stages and associations with other species of forensic interest

More than 85 % of *N. littoralis* specimens were found on decomposed cadavers (early to advanced decomposition), while such corpses represent less than 70 % of all forensic entomology cases. Such a preference for decomposed corpses was previously noted by Matuszewski, who demonstrated the link between temperature, decay stage, and pre-appearance interval [5, 7]. Ratcliffe reported the same requirement (active decay carcasses) for *N. surinamensis* larvae even if they were in some cases observed during dry decay stages.

Several other necrophagous species were closely associated with *N. littoralis*. These associated species included some pioneer Calliphoridae flies. As adult *N. littoralis* are feeding on carrion and maggots, their simultaneous presence on cadavers is not surprising [12]. A strong association was also observed with Fanniidae/Muscidae flies. These insects are usually considered to be later species, colonizing cadavers after Calliphoridae flies and mainly during the active decay stage [2, 16, 20, 26, 27]. The over-representation of these species among the *N. littoralis* cases may be explained by similar requirements regarding the decomposition stage of the corpse. According to this idea, Matuszewski observed during field experiments that *N. littoralis* adults colonized pig carcasses after Calliphoridae and Muscidae adults flies, but during the development of their larvae on the cadaver [5, 24]. We also observed a significant association with *Chrysomya albiceps* and *Phormia regina*. As these species are heliophilic and require a high temperature to develop successfully [28, 29], it is interesting to find them simultaneously with *N. littoralis*, which we observed to have the same requirement. Conversely, *N. littoralis* was rarely observed with *Calliphora vicina*, which is known as a cold-adapted species [26, 30].

N. littoralis was also found to be closely associated with several Coleoptera species, especially *Necrobia* spp., *C. maxillosus*, *Saprinus* spp., and other Silphidae. As most of these species are predators of fly larvae, we supposed that they are also attracted by the larval masses upon which they feed. The close association with *Dermestes* spp. was more surprising, as these insects usually feed on dry materials, i.e., after the decaying stages occurred [31, 32]. However, Ratcliffe reported that although primarily predators of maggots, *N. surinamensis* can subsist on flesh alone, feeding on dried skin and muscle, which are also consumed by dermestids [12, 32–34]. Furthermore, *N. surinamensis* was occasionally observed feeding on dermestid larvae [12].

Finally, forensic examiners reported that several corpses were heavily infested with thousands of *N. littoralis* larvae and adults feeding simultaneously on them. In one particular case (September, forest area, nighttime), so many adults were crawling around and underneath the cadaver that the corpse and the soil seemed to be moving (personal communication). In such cases, other insect species were scarcely represented, likely due to their predation by *N. littoralis*. This is especially true as *Necrodes* beetles can pick up and drop several maggots before eating one [12].

To conclude, the ecological preferences of *N. littoralis* inferred from this dataset of French forensic entomology cases from 1990 to 2013 can be summarized as follows:

1. *N. littoralis* has been observed throughout the French territory and Europe and is not restricted to the coastal areas.
2. *N. littoralis* is mostly an outdoor species (more than 90 % of cases).
3. *N. littoralis* has a strong seasonality and prefers warm weather conditions (87 % of cases between June and October).
4. *N. littoralis* is predominantly present during early to advanced decomposition stages.
5. *N. littoralis* is frequently associated with heliophilic flies, such as *C. albiceps* and *P. regina*, with Muscidae and Fanniidae, and with predatory or necrophagous beetles (*Necrobia* spp., *C. maxillosus*, *Saprinus* spp., and Silphidae).

As *N. littoralis* is observed, on average, in one case out of eight and has become more common during the last years, developmental data for this species would be a precious tool for forensic entomologists in Europe.

Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

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References

1. Frątczak K, Matuszewski S (2014) Instar determination in forensically useful beetles *Necrodes littoralis* (Silphidae) and *Creophilus*

- maxillosus* (Staphylinidae). *Forensic Sci Int* 241:20–26. doi:10.1016/j.foresciint.2014.04.026
2. Matuszewski S, Bajerlein D, Konwerski S, Szpila K (2008) An initial study of insect succession and carrion decomposition in various forest habitats of Central Europe. *Forensic Sci Int* 180:61–9
 3. Anton E, Niederegger S, Beutel RG (2011) Beetles and flies collected on pig carrion in an experimental setting in Thuringia and their forensic implications. *Med Vet Entomol* 25:353–364. doi:10.1111/j.1365-2915.2011.00975.x
 4. Dekeirsschieter J, Verheggen FJ, Haubruge E, Brostaux Y (2011) Carrion beetles visiting pig carcasses during early spring in urban, forest and agricultural biotopes of Western Europe. *J Insect Sci Online* 11:73. doi:10.1673/031.011.7301
 5. Matuszewski S (2011) Estimating the pre-appearance interval from temperature in *Necrodes littoralis* L. (Coleoptera: Silphidae). *Forensic Sci Int* 212:180–188. doi:10.1016/j.foresciint.2011.06.010
 6. Perez AE, Haskell NH, Wells JD (2014) Evaluating the utility of hexapod species for calculating a confidence interval about a succession based postmortem interval estimate. *Forensic Sci Int* 241: 91–95
 7. Matuszewski S, Szafałowicz M (2013) Temperature-dependent appearance of forensically useful beetles on carcasses. *Forensic Sci Int* 229:92–99
 8. Tabor KL, Brewster CC, Fell RD (2004) Analysis of the successional patterns of insects on carrion in southwest Virginia. *J Med Entomol* 41:785–795
 9. Prado e Castro C, García MD, Martins da Silva P, Faria e Silva I, Serrano A (2013) Coleoptera of forensic interest: a study of seasonal community composition and succession in Lisbon, Portugal. *Forensic Sci Int* 232:73–83
 10. Özdemir S, Sert O (2009) Determination of Coleoptera fauna on carcasses in Ankara province, Turkey. *Forensic Sci Int* 183:24–32
 11. Matuszewski S, Szafałowicz M, Jarmusz M (2013) Insects colonising carcasses in open and forest habitats of Central Europe: search for indicators of corpse relocation. *Forensic Sci Int* 231:234–239
 12. Ratcliffe BC (1972) The natural history of *Necrodes surinamensis* (Fabr.) (Coleoptera: Silphidae). *Trans Am Entomol Soc* 98:359–410
 13. Johansen H, Solum M, Knudsen GK, Hågvar E, Norli H, Aak A (2014) Blow fly responses to semiochemicals produced by decaying carcasses. *Med Vet Entomol* 28:26–34
 14. Dekeirsschieter J, Frederickx C, Lognay G, Brostaux Y, Verheggen F, Haubruge E (2013) Electrophysiological and behavioral responses of *Thanatophilus sinuatus* Fabricius (Coleoptera: Silphidae) to selected cadaveric volatile organic compounds. *J Forensic Sci* 58:917–923
 15. Von Hoermann C, Ruther J, Reibe S, Madea B, Ayasse M (2011) The importance of carcass volatiles as attractants for the hide beetle *Dermestes maculatus* (De Geer). *Forensic Sci Int* 212:173–179
 16. Smith KGV (1986) A manual of forensic entomology. Trustees of the British Museum (Natural History), London
 17. Matuszewski S, Konwerski S, Frączak K, Szafałowicz M (2014) Effect of body mass and clothing on decomposition of pig carcasses. *Int J Legal Med* 128:1039–48
 18. Matuszewski S, Bajerlein D, Konwerski S, Szpila K (2010) Insect succession and carrion decomposition in selected forests of Central Europe. Part 1: pattern and rate of decomposition. *Forensic Sci Int* 194:85–93
 19. Matuszewski S, Bajerlein D, Konwerski S, Szpila K (2010) Insect succession and carrion decomposition in selected forests of Central Europe. Part 2: composition and residency patterns of carrion fauna. *Forensic Sci Int* 195:42–51
 20. Easton AM, Smith KG (1970) The entomology of the cadaver. *Med Sci Law* 10:208–215
 21. Dekeirsschieter J, Frederickx C, Verheggen F, Boxho P, Haubruge E (2013) Forensic entomology investigations from Doctor Marcel Leclercq (1924–2008): a review of cases from 1969 to 2005. *J Med Entomol* 50:935–954
 22. <http://www.faunaeur.org/> (2015) *Necrodes littoralis* in Europe
 23. <https://data.nbn.org.uk> (2015) *Necrodes littoralis* in Great Britain and Ireland
 24. Matuszewski S, Bajerlein D, Konwerski S, Szpila K (2011) Insect succession and carrion decomposition in selected forests of Central Europe. Part 3: succession of carrion fauna. *Forensic Sci Int* 207: 150–163. doi:10.1016/j.foresciint.2010.09.022
 25. Lingafelter SW (1995) Diversity, habitat preferences, and seasonality of Kansas carrion beetles (Coleoptera: Silphidae). *J Kans Entomol Soc* 68:214–23
 26. Davies L, Ratcliffe GG (1994) Development rates of some pre-adult stages in blowflies with reference to low temperatures. *Med Vet Entomol* 8:245–54
 27. Johnson WT, Venard CE (1957) Observations on the biology and morphology of *Ophyra aenescens* (Diptera: Muscidae). *Ohio J Sci* 57:21–6
 28. Grassberger M, Friedrich E, Reiter C (2003) The blowfly *Chrysomya albiceps* (Wiedemann) (Diptera: Calliphoridae) as a new forensic indicator in Central Europe. *Int J Legal Med* 117: 75–81
 29. Byrd JH, Allen JC (2001) The development of the black blow fly, *Phormia regina* (Meigen). *Forensic Sci Int* 120:79–88
 30. Baqué M, Filmann N, Verhoff MA, Amendt J (2015) Establishment of developmental charts for the larvae of the blow fly *Calliphora vicina* using quantile regression. *Forensic Sci Int* 248:1–9
 31. Dekeirsschieter J, Stefanuto P-H, Brasseur C, Haubruge E, Focant J-F (2012) Enhanced characterization of the smell of death by comprehensive two-dimensional gas chromatography-time-of-flight mass spectrometry (GCxGC-TOFMS). *PLoS One* 7:e39005
 32. Charabidze D, Colard T, Vincent B, Pasquerault T, Hedouin V (2013) Involvement of larder beetles (Coleoptera: Dermestidae) on human cadavers: a review of 81 forensic cases. *Int J Legal Med* 128:1021–30
 33. Amos TG (1968) Some laboratory observations on the rates of development, mortality and oviposition of *Dermestes frischii* (Kug.) (Col., Dermestidae). *J Stored Prod Res* 4:103–117
 34. Coombs CW (1979) The effect of temperature and humidity upon the development and fecundity of *Dermestes haemorrhoidalis* Küster and *Dermestes peruvianus* Laporte De Castelnau (Coleoptera: Dermestidae). *J Stored Prod Res* 15:43–52