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Author

Spilmont, Nicolas, Gothland, Moana, Seuront, Laurent

Published

2015

Journal Title

Aquatic Invasions

Version

Version of Record (VoR)

DOI

[10.3391/ai.2015.10.3.07](https://doi.org/10.3391/ai.2015.10.3.07)

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Research Article

Exogenous control of the feeding activity in the invasive Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835)

Nicolas Spilmont^{1,2,3*}, Moâna Gothland^{1,2} and Laurent Seuront^{2,4}¹Univ. Lille 1, Laboratoire d'Océanologie et Géosciences, Station Marine de Wimereux, 28 av. Foch, BP 80, F-62930 Wimereux, France²CNRS, UMR 8187 LOG, 28 av. Foch, F-62930 Wimereux, France³Environmental Futures Research Institute, Griffith University, Gold Coast Campus, QLD 4222, Australia⁴School of Biological Sciences, Flinders University, Adelaide, SA 5001, Australia

*Corresponding author

E-mail: nicolas.spilmont@univ-lille1.fr

Received: 20 January 2015 / Accepted: 23 April 2015 / Published online: 14 May 2015

Handling editor: Melisa Wong

Abstract

The Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835) is an invasive decapod along the coast of the English Channel and the North Sea where it is displacing the indigenous European green crab *Carcinus maenas*. Although behavioural traits have been identified as a critical component of invasion success, they remain poorly studied in *H. sanguineus*. Hence, the present study quantitatively assessed the feeding activity of *H. sanguineus* in the laboratory under different light and starvation conditions. Non-starved *H. sanguineus* exhibited an exogenous day-night rhythm driven by a photophobic behaviour. Starved individuals lacked the photophobic behaviour, which may allow *H. sanguineus* to spend more time foraging than species characterised by true endogenous rhythms. Altogether, the foraging behaviours reported in this work highlight the behavioural flexibility and adaptive nature of this species, which may confer to *H. sanguineus* a competitive advantage in intertidal environments.

Key words: decapod crustacean, adaptive flexibility hypothesis, ntertidal, behavioural plasticity

Introduction

The combined effect of climate change and alien-species introduction is a key driver of biodiversity loss (Occhipinti-Ambrogi 2007; Mainka and Howard 2010). The spread of alien marine species is mainly due to the transport of larval stages *via* displacement of cultivated species (mainly bivalves) or in ballast waters (Occhipinti-Ambrogi 2007; Hänfling et al. 2011). Crustaceans are considered to be one of the most successful groups of aquatic invasive species (Hänfling et al. 2011). Crabs (i.e. brachyuran and 'crab-like' anomouran decapods) are particularly successful in estuarine and marine environments, with 73 species known to occur outside of their native ranges (Brockerhoff and McLay 2011). A combination of biological and physiological characteristics (eurytolerance, omnivory, and life-history traits;

Hänfling et al. 2011) are thought to explain their success. Adaptive behavioural traits also appear to have an important role in this invasion success (Holway and Suarez 1999; Weis 2010) and this behavioural plasticity has been termed the 'adaptive flexibility hypothesis' (Wright et al. 2010).

The Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835) was introduced to the Atlantic coasts of North America and Europe during the 1990's, and it is suspected to negatively affect intertidal communities *via* food web disruption (Brousseau et al. 2001). *H. sanguineus* was first reported in France in 1999 and has subsequently colonised the European Atlantic coast from the Cotentin Peninsular to the Wadden Sea (Gothland et al. 2013; Landschoff et al. 2013); where it is progressively displacing the European green crab *Carcinus maenas* (Linnaeus, 1758) (Dauvin and Dufossé 2011; van den Brink et al. 2012). The

competitive dominance of *H. sanguineus* over other crab species, including *C. maenas*, is well documented for the Atlantic coast of the US where both species are non-native (reviewed by Epifanio 2013). Reasons identified for the success of the Asian shore crab are as diverse as dominance for rock shelter, high adult mobility and low site fidelity, and aspects of their foraging behaviour (Brousseau et al. 2002; Jensen et al. 2002; Griffen et al. 2012). Due to its recent introduction, *Hemigrapsus sanguineus* has, to our knowledge, never been specifically examined in terms of behaviour in the European invasion range. It is, however, critical to understand the behaviour (e.g. tidal migrations, feeding preferences and rhythms) of non-native and indigenous species since there are competitive differences both between introduced and native species and between native and introduced populations of the same species (Weis 2010). As such, results obtained on the US coast cannot directly be extrapolated to the European case. Most intertidal crustaceans exhibit endogenous circadian rhythms of activity (DeCoursey 1983); this has, however, to our knowledge never been examined for *Hemigrapsus sanguineus*. Hence, the aim of the present study was to investigate the feeding activity of the Asian shore crab under different light conditions, both in starved and non-starved conditions, to assess the existence of a day-night rhythm and the potential ability of the species to modulate this rhythm.

Materials and methods

Adults of *Hemigrapsus sanguineus* (carapace width (CW) > 12 mm; McDermott 1998) were collected manually at several occasions in autumn (October 2012) at "Fort de Croy" (Wimereux, France: 50°45.766' N, 1°35.962' E). At this recently colonised site, abundances reached *ca.* 300 individuals under 30 boulders (Gothland et al. 2013). Individuals were collected in the mid-littoral during early morning receding tide, hence assumed to have their guts full (Griffen et al. 2012). Animals were brought back to the laboratory (LOG, Station Marine de Wimereux), sex determined, and males and non-ovigerous females were kept in separate aquaria with running natural seawater at *in situ* temperature (12°C). A batch of individuals was kept unfed for seven days before the experimental trials (starved individuals), whereas another batch was used during the appropriate high tide (considering

experimental conditions, see below) that followed collection.

For the experimental trials, non-moulting individuals of each sex were individually isolated in small aquaria (16.0 cm × 9.5 cm × 10.5 cm) filled with 6 cm of seawater. After 15 min of acclimatization, crabs were offered a crushed mussel (*Mytilus edulis*, mean shell length 36.3 ± 3.1 mm, mean ± S.D., n = 192). Experiments were conducted at constant seawater temperature (12 ± 1°C, mean ± S.D., n = 4), during hours of natural high tide, with 12 non-starved and starved individuals of each sex, i.e. a total of 48 tanks for each experimental condition. The behaviour of each crab was recorded for one hour using an infrared digital camera (DV Sony DCR-PC120E) (i) during daylight hours under natural sunlight conditions (daylight experiment, DE), (ii) during the night in the dark (night experiment, NE), (iii) during daylight hours in the dark (simulated night experiment, SNE), and (iv) during the night under simulated daylight conditions (cool white fluorescent light; simulated daylight experiment, SDE). After the experiments, the carapace width (CW) of each crab was measured. A total of 192 individuals (48 tanks × 4 experimental conditions) with intact chelae were used (CW = 16.6 ± 3.3 mm, mean ± S.D.), each experimental individual being used only once. To ensure the independence of the trials, after each experiment aquaria were washed with seawater, quickly rinsed with 95% ethanol, then with distilled water (3 times) and were allowed to dry until the next experiment.

The video clips were inspected by a single person to standardize and ensure consistency. The response time, R_t , was defined as the time elapsed (s) between the introduction of the mussel in the experimental container and the first physical contact that led to mussel consumption. $R_t > 3600$ s was recorded when an individual did not feed during the one-hour trial. Only clips where the consumption of mussel tissue was clearly seen were used (12 clips were discarded due to poor video quality). Due to non-normal distributions and to the use of semi-quantitative data (i.e. use of an ordinal scale for > 3600 s), nonparametric statistical tests were used. Comparisons between two samples were conducted using the Mann-Whitney *U*-test (MW test hereafter), and multiple comparisons between treatments using the Kruskal-Wallis *H*-test (KW test hereafter) and a subsequent non-parametric multiple comparison procedure was used to identify distinct groups of measurements (Zar 1999).

Results

No statistical difference was detected between male and female response time R_t in any experiment (MW tests, $p > 0.05$); therefore, the data from males and females were combined.

The observed response time of non-starved *H. sanguineus* (Figure 1) varied between 7 s (SNE) and > 3600 s (DE and SDE). The longest R_t within the one-hour observation window was for DE (*i.e.* 2938 s). R_t in dark conditions (NE and SNE) was significantly faster than in light conditions (DE and SDE; KW test, $p < 0.05$). In both NE and SNE, more than 85% of the individuals fed within the first 600 s, whereas only 32% and 58% did during DE and SDE, respectively.

There was no significant difference between treatments for the experiments conducted on starved individuals (Figure 2; KW test, $p > 0.05$). For each experimental condition, R_t was significantly faster for starved than non-starved animals (MW tests, $p > 0.05$). Excluding the one individual that did not feed over the trial duration (under natural light conditions), R_t ranged from 3 s (NE) to 1309 s (SDE). In all experimental conditions, more than 90% of the starved individuals fed within 600 s for DE, SDE and NE, and even all of them for SNE.

Discussion

Hemigrapsus sanguineus has long been considered to forage more actively during high tide and in darkness (Depledge 1984; Saigusa and Kawagoye 1997; Brousseau et al. 2002). This mainly relied on personal observations or indirect evidence from other activities, such as larval release (Saigusa and Kawagoye 1997) or cardiac activity (Depledge 1984). In contrast, the present study quantitatively assessed the feeding activity of *H. sanguineus* under different light conditions. Our results show that this species exhibits a non-endogenous day-night rhythm, since it fed more actively in dark conditions, either during the day or at night (Figure 1); this basic photophobic behaviour may constitute an adaptive advantage for *H. sanguineus* as an invasive species when competing with species characterised by endogeneous rhythms. We also showed that *H. sanguineus* exhibited behavioural plasticity, since photophobia was not expressed under starvation (Figure 2). This flexibility may represent another competitive advantage in locally or temporarily

food-depleted environments, but could be more accurately tested by investigating the stress generated by increasing starvation durations. The behavioural properties identified in this work are likely to provide a new mechanistic explanation for the success of the invasion of the Asian shore crab in intertidal rocky substrates of the eastern English Channel (Dauvin and Dufossé 2011; Gothland et al. 2013) and the North Sea (van den Brink et al. 2012; Landschoff et al. 2013).

In contrast, the activity of *C. maenas* is driven by an endogenous circadian rhythm (Arechiga et al. 1974; Reid and Naylor 1989; Aagaard et al. 1995), combined with instinctive light avoidance (Orlosk et al. 2011). In high turbidity areas, such as the eastern English Channel where light extinction is in the 80–99% range for intertidal organisms during high tide (Spilmont et al. 2009), dark conditions may occur even during daylight high tides (simulated in our SDE experiments). A photophobic species such as *H. sanguineus* would hence actively feed during dark conditions whether they occur during daylight hours or at night, in contrast to a species driven by an endogenous rhythm such as *C. maenas*. *Hemigrapsus sanguineus* would consequently spend more time foraging than *C. maenas*, which, considering their similar diet and feeding rates (Jensen et al. 2002; Lohrer and Whitlatch 2002; DeGraaf and Tyrrell 2004; Tyrrell et al. 2006), would confer a strong competitive advantage to *H. sanguineus* over *C. maenas* where adults of both species coexist. However, some studies also suggested plasticity in *C. maenas*. Indeed, Orlosk et al. (2011) showed that individuals could be conditioned against natural light avoidance, whereas Aagaard et al. (1995) observed *C. maenas* individuals foraging at night (though most foraged during the day). Besides, spending more time foraging (as suggested here for *H. sanguineus*) would increase both energy expenditure and predation risk, particularly in daylight conditions. Predation risk is likely to be relevant since *H. sanguineus* is preyed upon preferentially by native crustacean-eating fishes (Heinonen and Auster 2012). Thus, behavioural plasticity alone could not explain the invasion success of *H. sanguineus*, which is more likely the result of several mechanisms, including foraging behaviour, reproductive success, competition for shelter and food, and predation on juveniles of native species (Epifanio 2013). This might be particularly true for the site studied in the present work where *C. maenas* adult individuals were abundant in the mid-littoral in the late 1990s/early

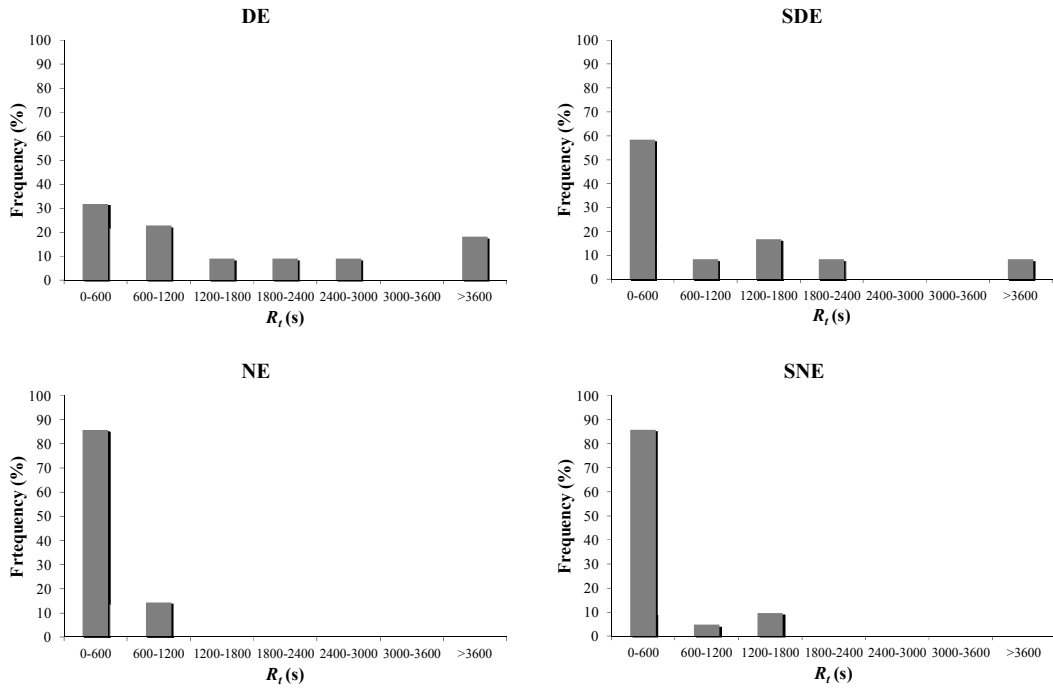


Figure 1. Frequency distribution of the response time, R_t , of non-starved *Hemigrapsus sanguineus* to a crushed mussel under natural (DE, day experiment n = 22; NE, night experiment n = 21) and un-natural (SDE, simulated day experiment n = 24; SNE, simulated night experiment n = 20) experimental conditions.

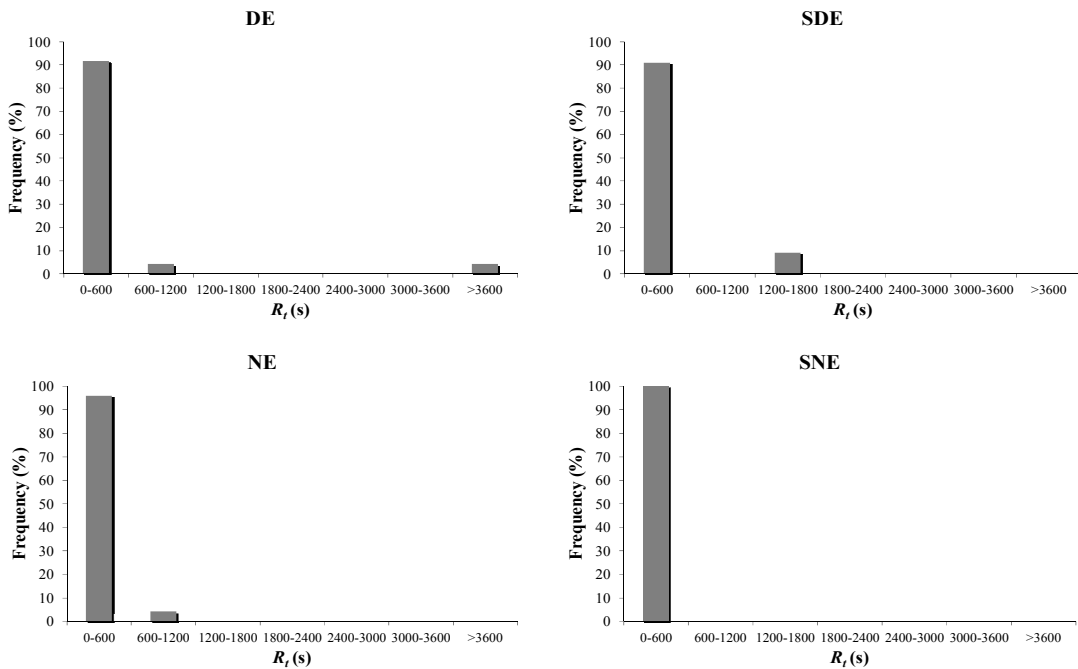


Figure 2. Frequency distribution of the response time, R_t , of starved *Hemigrapsus sanguineus* to a crushed mussel under natural (DE, day experiment n = 24; NE, night experiment n = 24) and un-natural (SDE, simulated day experiment n = 23; SNE, simulated night experiment n = 22) experimental conditions.

2000s (N. Spilmont, pers. obs.) whereas abundances are now low (ca. 20 individuals under 30 boulders: Gothland 2013), evidence for competitive displacement or a predator-prey interaction, which are not mutually exclusive hypotheses. These hypotheses would need additional work, including a study of the feeding activity of *C. maenas* using the same experimental procedure (together with direct field observation when possible) which was, however, impossible to conduct due to the limited number of adult European green crabs found in the field.

The results presented here are a first step in the understanding of *H. sanguineus* foraging behaviour in its European invasion range and there are some limitations in the experimental design that limit the use of the results to model field behaviour and predict ecosystem consequences related to *H. sanguineus* becoming established in a location. Indeed, the behaviour was examined in conditions where the crabs used mussel tissues that did not require opening or cracking the mollusc shells and the response may differ depending on the interaction of group dynamic and prey size or type. *Hemigrapsus* individuals often occur together and there may be a suite of different decisions about foraging behaviour within a group of individuals and when they have to kill their prey.

Our results are also relevant to recently introduced populations as the behaviour of invasive *H. sanguineus* may differ from both native (Weiss 2010) and long-established invasive populations (Rossong et al. 2012). Note that potential genetic differences at regional scales have also been suggested to trigger behavioural differences (Rossong et al. 2012). The potential genetic diversity of introduced *H. sanguineus* populations is however still unknown along the coasts of Northern European. The resolution of this issue is however well beyond the scope of the present work, but stresses the need for additional studies to examine the potential role of genetics in the origin of the observed behavioural differences. A first step towards the generalisation of the behaviour reported here would need a thorough behavioural assessment of individuals sampled at several introduction locations. Our results, however, show that *H. sanguineus* exhibits a singular exogenous flexible activity rhythm, hence provide a good example of the 'adaptive flexibility hypothesis' (Wright et al. 2010) typical of invasive species.

Acknowledgements

Thanks are due to A. Hachet for technical help during the experiments, to anonymous reviewers, associate editor, and co-editor in chief for their comments on the manuscript. This study received financial support from the French national program EC2CO through a project titled 'Colonisation des côtes par deux espèces du genre *Hemigrapsus*: origine, état des lieux et compétition interspécifique en Manche/Mer du Nord'.

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