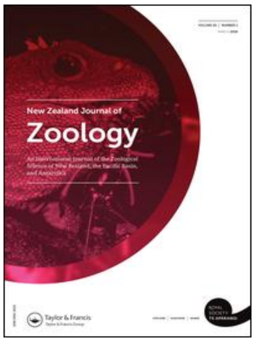

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Unexpected meal: first record of predation upon a potentially neurotoxic sea slug by the European green crab *Carcinus maenas*

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ABSTRACT

An unexpected predator-prey interaction is reported between two successful invasive species in Patagonia, the European green crab *Carcinus maenas* (Linnaeus, 1758) and the potentially neurotoxic grey side-gilled sea slug *Pleurobranchaea maculata* (Quoy & Gaimard, 1832). On two different occasions, a total of four crabs were observed preying upon the sea slugs in the field. The establishment of a novel predator-prey interaction between these species can imply significant effects on their potential spread and invasive success along the South Western Atlantic, as well as it provides a noteworthy contribution towards the knowledge of the currently underexplored question related to what eats the sea slugs.

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Introduction

Unlike most marine gastropods that rely on a hard protective shell to avoid predation, Heterobranch sea slugs have developed various morpho-physiological anti-predator strategies (Wägele and Klussmann-Kolb 2005). These include chemical defenses (Wägele et al. 2006; Avila et al. 2018), active escape swimming (Mauzey et al. 1968), aposematism (Gosliner 2001), a cryptic appearance (Wägele and Klussmann-Kolb 2005) or ink secretion (Derby 2007). Both empirical observations and experimental data suggest that predation on Heterobranch sea slugs is rare (Valdés et al. 2013). However, a number of diverse organisms have been reported feeding on sea slugs, including anthozoans (Van der Meij and Reijnen 2012; Mehrotra et al. 2019), crabs (Trowbridge 1994), sea stars (Mauzey et al. 1968) and pycnogonids (Arango and Brodie 2003), among others. In addition, many reports of predation upon sea slugs are often concealed in non-malacological literature and are very difficult to trace (Rudman 2000). For example, prey lists derived from stomach content analyses of fish (Bielsa and Labisky 1987; Yang and Nelson 1999; Loury 2011), crabs (Vannini et al. 1989) or octopuses (Rosas-Luis et al. 2019) occasionally include sea slugs as occasional prey

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items. Thus, even though predation events upon sea slugs are certainly rare, they can also be largely underestimated by the scarcity of specific literature.

The grey side-gilled sea slug (*Pleurobranchaea maculata* [Quoy & Gaimard, 1832]) was recently introduced in Argentine Patagonia (Farías et al. 2015, 2016), where it is considered a highly invasive species due to its rapid spread (Battini in press). Native to New Zealand and South Western Australia, this species secretes extremely acidic mucus composed of sulfuric acid (Avila et al. 2018) when disturbed. In addition, it can accumulate highly variable concentrations of potent neurotoxins, such as tetrodotoxin and saxitoxin, most likely from toxic prey (McNabb et al. 2010; Wood et al. 2012; Salvitti et al. 2017; Farías et al. 2019). These substances have been proposed as chemical defense mechanisms to avoid potential predators (Wood et al. 2012; Khor et al. 2014). Indeed, to our knowledge, no records of predation upon this species have been published other than cannibalistic interactions with other specimens of *P. maculata* (Taylor et al. 2015; Bökenhans et al. 2019). Based on aquarium and field experiments, the absence of predators has been regarded as one of the main reasons for the invasive success of this species along the South Western Atlantic (Battini in press). In this work, we provide the first *in situ* evidence of predation on *P. maculata* by the also non-native European green crab (*Carcinus maenas* [Linnaeus, 1758]). Additionally, this represents the first report of predation upon sea slugs by this highly invasive and thoroughly studied marine predator.

Material and methods

The predatory interactions between the European green crab *Carcinus maenas* and the grey side-gilled sea slug *Pleurobranchaea maculata* were observed on two occasions by SCUBA diving on the southern coast of the Nuevo gulf (42°50′01″ S 64°52′12″ W), in northern Argentine Patagonia. In the first one (29 October 2018), one of us (NB) found one crab holding the remains of an already partially consumed *P. maculata* within its claws at a depth of 6 m. Unfortunately, no photographic records were made from that event. On the second occasion (07 November 2020), three individuals of *C. maenas* were found preying on *P. maculata* during a single dive in the southern coast of the Nuevo gulf at a depth of 3 m. Two of these events were photographically recorded and both sea slugs and crabs were identified *in situ*, so no specimens were collected. Two slugs were easily identifiable due to the early consumption stage, while the third one was already mostly consumed and it was necessary to disturb the crab in order to positively identify the prey.

Results

In all cases, the crabs were found holding the sea slugs with one or both claws (Figure 1A), with which they were passed directly to the maxillipeds (Figure 1B) that gradually tore off small pieces of tissue that were ultimately ingested (Figure 1C). On one occasion, half of the body of a sea slug poked out the mouth, while the other half was probably already eaten by the crab. All the sea slugs appeared dead at the time the observations were made, with severe wounds probably produced by the crab's claws. Unfortunately, we were unable to see the crabs attacking the sea slugs, so it is possible that they were dead prior to the capture. However, we did not see any other dead slugs during the

Figure 1. A, Green crabs *Carcinus maenas* preying on *Pleurobranchaea maculata*. **A**, The crab holds the partially consumed sea slug between its claws before **B**, consuming its viscera. **C**, A second crab feeding on another sea slug, showing signs of being already more consumed than the in a–b.

dive, so there is also a possibility that they were captured alive. In addition, it was impossible to remain observing the crabs until they finished their meal, but the different consumption stages among the three individual preys suggests that they probably consumed the entire sea slug after we saw them.

Discussion

The predation events upon *Pleurobranchaea maculata* reported herein were extremely unexpected based on prior field observations and experimental evidence (Battini in press). The green crab *Carcinus maenas* was introduced in the South Western Atlantic around 1999 (Hidalgo et al. 2005), but it reached the area of the Nuevo gulf in 2015 (Torres and González-Pisani 2016), a few years later than *P. maculata* (Battini 2016, in press). Rapidly, it became increasingly abundant throughout the gulf, inhabiting all types of coastal areas and probably affecting various species and threatening the ecological intertidal and subtidal communities of Patagonia (Battini and Bortolus 2020). Upon detection, the feeding behaviour of *C. maenas* has been regularly monitored through SCUBA field observations, during which several prey species were identified, including shelled gastropods [*Tegula patagonica* (d'Orbigny, 1835)], bivalves [*Brachidontes rodriguezii* (d'Orbigny, 1842), *Perumytilus purpuratus* (Lamarck, 1819), *Mytilus* spp.], unidentified Echiura, crabs (*Cyrtograpsus* spp.), cirripedians (*Balanus glandula* Darwin 1854) and echinoderms [*Arbacia dufresnii* (Blainville, 1825)] among others (pers.

observation). Recently, a more detailed assessment including metabarcoding, stomach content, and stable isotope analyses revealed a highly diverse diet for *C. maenas* (Cordone et al. in press) Although this species is among the most successful invasive species worldwide (Lowe et al. 2004), and it is known for its predatory voracity and diversity of prey (Le Roux et al. 1990; Baeta et al. 2006), previous evidence indicated that it did not feed on *P. maculata* (Battini in press). Even in areas that are frequented by divers, where crabs and sea slugs were both abundant, no prior predation events were reported. Indeed, specific predator-prey aquarium experiments between *C. maenas* and *P. maculata* indicated that the latter was not a potential prey (Battini in press). Thus, the first observation in 2018 was regarded as a rare exception, but later findings in 2020 suggest that it may have become a more common interaction in the area.

These observations of crabs eating sea slugs can reflect that a novel predator-prey interaction may have been established. Dietary shifts of predators in response to novel prey have been studied mostly in terrestrial predators (Phillips and Shine 2006; Carlsson et al. 2009; Llewelyn et al. 2014). For example, invasive rats shift from a seabird-based diet to other prey when the former are scarce, outside the breeding season (Caut et al. 2008). In the Nuevo gulf, native mussels and crabs inhabiting rocky intertidal and shallow subtidal have significantly declined following the introduction of *C. maenas* (Mendez et al. in press). Although factors other than just predation by *C. maenas* are probably involved in this decline, reduced food availability may explain the assimilation of novel prey sources by this successful predator. Alternatively, the rapid adaptation of behavioural or morphological traits might have also favoured a dietary shift to exploit *P. maculata* as a novel prey, which is very abundant in the Nuevo gulf. Previous studies suggest that *C. maenas* can learn to handle novel prey items (Hughes and O'Brien 2001), and even that those behavioural shifts can favour morphological changes (Edgell and Rochette 2009).

Alternatively, as we were unable to observe any event in which the crabs attacked the sea slugs prior to consumption, there is a possibility that the latter were already dead when captured. These sea slugs are frequently washed away to the shore (McNabb et al. 2010; Battini 2016), probably due to strong currents, and subsequent tidal events could drag dead individuals in-water again, where they could have been captured by the crabs. If that was the case, it is likely that no acidic secretion from the mantle occurred, which could have otherwise prevented predation, as suggested by previous experimental observations (Battini in press). Neurotoxins, on the other hand, are still active after prey death and so they could still act as antipredator compounds (Noguchi et al. 2011). However, these toxins probably act through a mechanism defined as 'toxicity following ingestion' (Caro and Ruxton 2019). Thus, as the effects of the toxins are slightly delayed from ingestion, this mechanism requires certain level of predator-prey eco-evolutionary experience to be effective (Caro and Ruxton 2019), which is improbable among species that have such a short period of coexistence. Finally, it is also likely that the sea slugs consumed by the crabs could have lacked these toxins, given the extremely variable concentrations among individuals (Salvitti et al. 2017; Farías et al. 2019).

Predator prey interactions are dynamic, especially when novel predators or preys are introduced (Saul et al. 2013). Here, we suggest that novel predator-prey interactions may have been established following the introduction of two marine species in northern Patagonia. Given that both species are the most successful marine invertebrates in the Nuevo gulf (Schwindt et al. 2018, 2020), that the prey can accumulate potent neurotoxins and that it has the potential to establish non-native populations worldwide (Battini et al. 2019), this observation will hopefully encourage further research concerning the effects that this novel interaction will produce in the invasive populations of both *C. maenas* and *P. maculata* in the South Western Atlantic as well as in other regions where both species can interact. Additionally, these observations highlight the importance of SCUBA diving as a valuable tool to unravel ecological interactions among marine species. This is the first field report of *C. maenas* feeding upon a sea slug, the second by a brachyuran crab (Anker and Ivanov 2020), adding important information on the biology and ecology of this widespread marine predator, as well as an important contribution towards filling the knowledge gap that exists in relation to the predators of sea slugs.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

No data set is associated with this paper.

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