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Hiding behaviour of *Oxynoe olivacea* (Mollusca: Opisthobranchia: Sacoglossa) in the invasive seaweed *Caulerpa taxifolia*

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Abstract

The occurrence of the invasive seaweed *Caulerpa taxifolia* in the Straits of Messina (Italy) provides an excellent opportunity to examine the spatial and temporal patterns of abundance of the endemic Mediterranean sacoglossan *Oxynoe olivacea*. Densities of this species were recorded in March, June and October 2000 on three different habitats: the underside of boulders (UNB), the upper side of boulders (UPB), and the surface of concrete blocks (CB). Results showed that in March, *O. olivacea* was consistently more abundant on UNB whereas in June it was present exclusively on CB. The density of *O. olivacea* was similar in the three habitats in October. The hiding behaviour of *O. olivacea* and its seeming disappearance in March did not coincide with a decline of abundance of phylloids of *C. taxifolia*. The results represent an important basis for further studies devoted to the investigation of abundance of these marine invertebrates, which has been traditionally thought of as unpredictable.

Keywords: *Opisthobranchia*, *habitat selection*, *Mediterranean sacoglossan*, *Caulerpa taxifolia*, *cryptic habits*

Introduction

In the past 20 years, there has been a rapid increase in studies on coastal marine invasions and ecological and evolutionary aspects of introduced species (Carlton & Geller 1993; Carlton 1996; Simberloff 2000; Grosholtz 2002; Glasby 2012). In particular, much attention has been addressed to the negative impacts of introduced marine macroalgae on altering native habitat and communities (Schaffelke et al. 2006; S.L. Williams & Smith 2007; Thomsen et al. 2009; Glasby 2012).

Species of the genus *Caulerpa* are the best known macroalgal invaders and, according to Glasby (2012), one of the better studied species is *Caulerpa taxifolia* (Vahl) C. Agardh.

From its first discovery in 1984 at the base of the Monaco aquarium (from where it was accidentally released), *C. taxifolia* has now spread throughout the western Mediterranean Sea, southeast Australia, Japan and southern California (Meinesz & Hesse 1991; Jousson et al. 2000; Cevik et al. 2012).

This invasive green alga is of particular concern because of its ability to propagate from asexual fragments and negative impacts on native habitat, fisheries and tourism in coastal communities (Meinesz & Hesse 1991; Relini et al. 2000; Ceccherelli et al. 2002).

However, the occurrence of *C. taxifolia* may have some beneficial roles in situations where there have been large-scale losses of similar native ecosystem engineer species (Crooks 2002; Rodriguez 2006). For example, this invader can also positively influence native species by providing new shelter, food and enhancing local biodiversity (Cevik et al. 2012). Trowbridge and Todd (2001) consider the geographic expansion of the invasive green alga *Codium fragile* ssp. *tomentosoides* (van Goor) Silva and *C. taxifolia* as a unique opportunity to study ecological and coevolutionary relationships, such as those that occur among shelled sacoglossan species and their algal hosts.

The opisthobranch order Sacoglossa is a relatively widespread group of oligophagous herbivores,

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comprising almost 300 described species (Jensen 1997). Evolution in this order has been closely linked to their specialized suctorial herbivorous habits. All the shelled species (about 20% of the described species) feed exclusively on green algae of the genus *Caulerpa*, being strongly entrained upon the life histories of *Caulerpa* spp. (Clark & DeFreese 1987; Jensen 1997; Williams & Walker 1999). Their functional specializations, such as modified teeth for piercing the cell wall of the food algae, kleptoplasty, sequestration of secondary metabolites from algae, cryptic morphology and colouration, suggest the “co-evolution” of these invertebrates and their algal host (Jensen 1997).

In this context, *Caulerpa* spp. invasions represent a precious opportunity to investigate the ecology of these marine specialist herbivores and their interactions with new possible host species. The Mediterranean invasion of the upright *C. taxifolia* has markedly expanded the geographic distribution range of the endemic sacoglossan *Oxynoe olivacea* Rafinesque, 1814. This species, that previously lived and foraged exclusively on the native *Caulerpa prolifera* (Forsskål) Lamouroux, is now found on stands of invasive species of *Caulerpa* (Thibaut & Meinesz 2000; Gianguzza et al. 2007).

Major features of *O. olivacea* are: the extreme stenophagy, the green and cryptic coloration attributable to the ingested chloroplasts, the presence of planktotrophic veliger larvae (Jensen 2001) and the capability of taking up and concentrating secondary metabolites from *Caulerpa* spp. which are used defensively (Cimino et al. 1990; Gavagnin et al. 1994).

To date, *O. olivacea*'s life span is unknown and information on its developmental history is scanty (Thibaut & Meinesz 2000). This simultaneous hermaphrodite may reach 40 mm in length, shows rapid sexual maturation (Gianguzza et al. 2004) and high spawning frequency (Thibaut & Meinesz 2000; Gianguzza et al. 2005). Exhaustive scrutiny of the literature shows that natural populations of this species occur in extremely low and often highly variable densities (Thibaut & Meinesz 2000; Gianguzza et al. 2004, 2007).

According to previous surveys conducted in 1999 at the Torre Faro's marina in the Straits of Messina (southern Italy), a consistent number of *O. olivacea* was easily visible actively crawling and feeding on *C. taxifolia* during the summer season. Unexpectedly, we noticed that *O. olivacea* often occurred under boulders covered by *C. taxifolia* during winter months. If these accidental observations reflect true temporal patterns of distribution, this might suggest that *O. olivacea* may select cryptic

habitats (*sensu* Schlagintweit & Bover-Arnal 2011) in determined times of the year, conditioning its apparent temporal and spatial patterns of abundance. This study sets out to establish if the presence of *O. olivacea* on three different habitats depends on the time of the year. We tested the hypothesis that *O. olivacea* density is not highly variable *per se* but it is affected by temporal change of habitat use (i.e. cryptic *vs* non cryptic habitat).

Material and methods

The study was carried out from March to October 2000 at the Torre Faro's marina in the Straits of Messina (38° 15.95' N; 15° 39.10' E Figure 1), where *C. taxifolia* was reported for the first time in the central Mediterranean Sea (Orestano et al. 1994). This mooring place covers an area of approximately 1.5 ha with a maximum depth of 8 m, and the bottom consists of a boulder field covered with *C. taxifolia*. Boulders are characterized by similar shape and size; their upper side is covered by *C. taxifolia*, while the underside is usually partly covered by sessile invertebrates (e.g. sponges, bryozoans) and by the rhizoids of *C. taxifolia*. Seventy cubic concrete blocks (2 m on a side), covered by *C. taxifolia*, form a breakwater parallel to the shore that marks the boundaries of the marina. Density of large *O. olivacea* specimens (body size from 20 to 35 mm) was estimated by independent visual counts in three different habitats: the underside of boulders (UNB), the upper side of boulders (UPB) and the surface of the concrete blocks (CB). Samplings were performed by scuba diving at three different times of the year (March, June and October 2000) characterized by different sea surface temperatures (average \pm d.s. $15.6 \pm 0.22^\circ\text{C}$, $19.89 \pm 0.86^\circ\text{C}$ and $21.59 \pm 0.56^\circ\text{C}$ respectively).

A total of 20 boulders (UNB and UPC, $n = 10$) were randomly sampled during each of the three months for a total of 60 observations. Densities of *O. olivacea* above and below boulders were independently estimated by counting the number of specimens occurring either on the top surface or on the bottom surface of each boulder, divided by the total estimated surface. Sampling was restricted to boulders with a horizontal top surface of about 30×15 cm and covered with *C. taxifolia*. Densities of *O. olivacea* on blocks were estimated by counting the number of specimens occurring within frames of 30×30 cm. Data from both boulders and blocks were standardized as number of specimens per square meter.

In order to determine possible changes in the abundance of *C. taxifolia* dependent on the time of the year, we evaluated the abundance of the algae

Table I. Results of the analysis of variance (ANOVA) on the effects of time (March vs June vs October) and habitat (the underside of boulders – UNB, the upper side of boulders – UPB, and the surface of the concrete blocks – CB) on densities of *Oxynoe olivacea*. SS – sum of squares; DF – degrees of freedom; MS – means square; F – F value; p – probability level.

Source	SS	DF	MS	F	P
Time (Ti)	0.6612	2	0.3306	1.89	0.1581
Habitat (Ha)	0.5720	2	0.2860	1.63	0.2018
Ti × Ha	83.162	4	20.790	11.87	0.0000
Residual	141.903	81	0.1752		
Total	237.397	89			

Transform: log-transformed. Cochran's Test C = 0.2023 (not significant) 0.2023.

from January 1999 to December 2000. Abundance of the algae was evaluated as density of phylloids in 0.25 m² randomly placed squares. The number of phylloids was counted monthly by scuba diving and five replicate measurements were taken on each sampling date.

Differences of *O. olivacea* density between habitat and month were tested by using an orthogonal two-way analysis of variance (ANOVA) model considering the following fixed factors: time of the year (Ti) as fixed factor with three levels: March, June and October; habitat (Ha) fixed factor with three levels: underside of boulder (UNB), upper side of boulder (UPB) and surface of concrete blocks (CB). Before running the analysis, the assumption of homogeneity of variances was examined using Cochran's C-test. Data were log-transformed prior to analysis (Table I). Student-Newman-Keuls (SNK) tests were used for *a posteriori* multiple comparisons of means (at $\alpha = 0.05$). The GMAV 5.0 software (University of Sydney, Australia) was used to perform the statistical tests.

Results

Density of large *O. olivacea* ranged from 0 [mean number of individuals per m² ± standard error (SE) on CB in March, UPB and UNB in June] to 4.7 ± 1.17 (mean number of individuals per m² ± SE on UNB in March, Figure 1). A detailed analysis of time and habitat effects on *O. olivacea* density is summarized in Table I. Results showed a significant effect of the term "Ti × Ha" (ANOVA F_{4,81} = 11.87, P < 0.00001, Table I). Post-hoc pairwise comparisons on this term indicated that in March, density of *O. olivacea* was higher on UNB than on UPC (mean number of individuals per m² ± SE: 4.7 ± 1.17 and

0.752 ± 0.4 respectively), whereas no *O. olivacea* was found on the CB habitat.

In June *O. olivacea* occurred exclusively on CB (mean number of individuals per m² ± SE: 3.5 ± 0.2), while in October no significant differences in density were detected among the three habitats.

The distribution of *O. olivacea* individuals among the three habitats across the different times of the year confirmed that *O. olivacea* adopts a cryptic behaviour in March, when animals hide below boulders and show a sleeping behaviour. It was very common to find two or three specimens very close to each other as a small herd. The animals appeared still and less green than usual. In June, specimens are easily visible actively feeding on *C. taxifolia* leaves. The abundance of phylloids of *C. taxifolia* increased gradually from May to October, showing a peak in October and a decline over the subsequent months until February (Figure 2).

Discussion

Annual cycles in population density have been demonstrated in several sacoglossans, mostly in temperate species where their disappearance is associated with drying out of temporary pools or die-back of food algae (Wilson & Forrest 2004). For example, abundance of *Elysia timida* (Risso, 1818) is highly controlled by the supply of the Chlorophyta *Acetabularia acetabulum* (L.) P.C. Silva (Marín & Ros 1992). However, predation, cryptic behaviour and spawning aggregations are also recognized as potential sources of variability for sacoglossan densities (Trowbridge 2002). For instance, *Alderia modesta* (Lovén, 1844) density can be significantly reduced by predators such as fish and crabs (Trowbridge 1993). Protective hiding behaviour has been described in the North American *Elysia catulus* (Gould, 1870), which feeds on seagrass and hides in fascicles of *Zostera marina* L. (Clark 1975). During the autumn and winter months, *Ascobulla ulla* (Marcus and Marcus, 1970), a tectibranch sacoglossan, shows an unusual burrowing behaviour and its apparent disappearance coincides with the seasonal decline of *C. racemosa*, its food source (De Freese 1987). In warmer waters, *Elysia tuca* Marcus and Marcus, 1967, an epifaunal sacoglossan feeding on *Halimeda* spp., may show changes in several features, including the retention of functional plastids, egg deposition, feeding rate and growth rate in relation to seasonal climatic factors (Waugh & Clark 1986).

In this preliminary study, significant effects of time and habitat on density of *O. olivacea* were detected. *O. olivacea* was significantly more abundant on the underside than on the upper side of the boulders

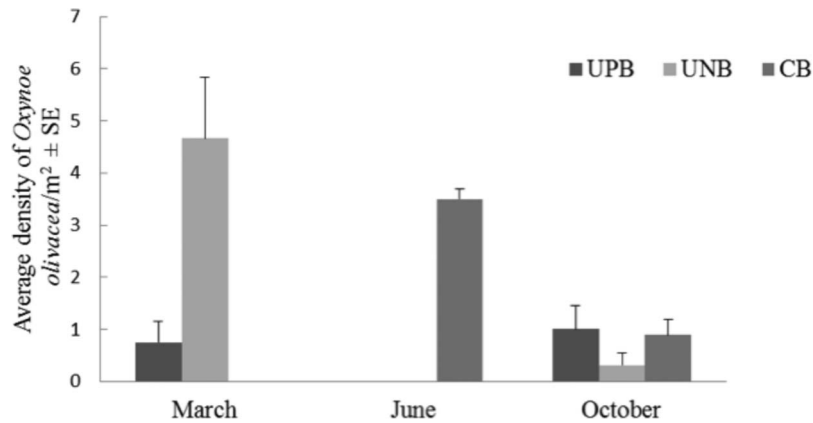


Figure 1. Densities \pm standard error (SE) of *Oxyntoe olivacea* at the three different habitats (underside of boulders – UNB, upper side of boulders – UPC and the surface of the concrete blocks – CB) and three different times of the year (March, June and October).

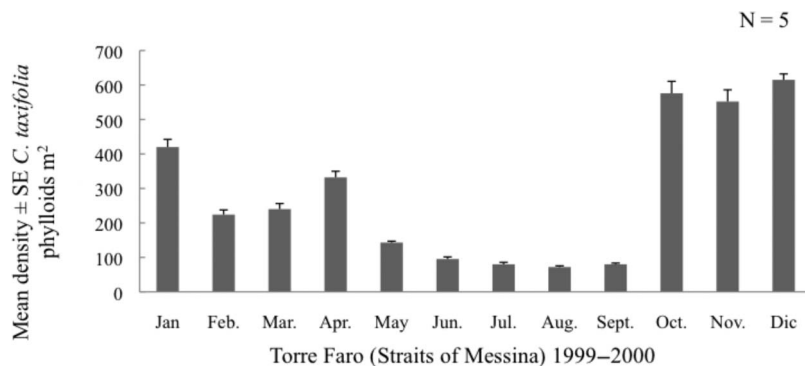


Figure 2. Monthly variation in abundance of phylloids of *Caulerpa taxifolia* (January 1999–December 2000). SE, standard error.

in March when no individuals were found on the surface of the concrete blocks. In June, *O. olivacea* was present exclusively on the surface of the blocks where it was actively feeding on *C. taxifolia* phylloids. Finally, in October, the density of *O. olivacea* was similar in the three habitats. The hiding behaviour of *O. olivacea* and its seeming disappearance in March did not coincide with a decline of abundance of phylloids of *C. taxifolia*. Perhaps the hiding behaviour of *O. olivacea* does not respond to extrinsic environmental factors, but may be determined by intrinsic factors derived from the co-evolution with *C. prolifera*, its ancestral food. This species, contrary to *C. taxifolia*, suffers from low temperatures (lower than 14°C), losing its phylloids and recovering them in the warmest months (Gavagnin et al. 1994). This could suggest that the hiding behaviour of this sacoglossan seems to be better coupled to phenology of *C. prolifera* more than to *C. taxifolia*.

Moreover, predation is not a controlling factor for *O. olivacea* populations, as the production of the noxious metabolites *oxytoxin-1* and *oxytoxin-2* makes this species unpalatable (Cimino et al. 1990; Marín &

Ros 2004; Cavas et al. 2005). Interestingly, *O. olivacea* showed a cryptic behaviour in March, hiding below the boulders and forming sleeping groups of two or three animals very close to each other. During field observations, the animals remain motionless side by side and do not respond to disturbances. This behaviour has already been described in *O. olivacea* as well as in *Lobiger serradifalci* as “sleeping behaviour”, and as feeding it is considered a gregarious activity (Sea Slug Forum 2004: <http://www.austmus.gov.au/seaslugs/net/list-6391.htm>), a way in which small consumers can successfully feed and stay on large, sedentary items, reducing individual risk of predation (Gianguzza et al. 2007).

In this study, a new and unusual behavior for *O. olivacea* was observed: in March this species hides below the boulders covered by *C. taxifolia*. Probably at this time of the year *O. olivacea*, unprotected by physical constraints of an external shell, prefers to stay in cryptic habitats such as the under-rock surface of boulders in order to avoid stressful environmental conditions such the local strong hydrodynamism. The Straits of Messina, as stated by Mosetti (1988),

during the winter season is often subjected to intense tidal currents of semidiurnal type (330 cm sec⁻¹ March 1980). The presence of very strong currents and severe wave disturbance associated with low temperatures could have a direct effect on the behaviour of *O. olivacea*. Probably this species emerged only briefly under the boulders, perhaps when the swell and waves were minimal, just to feed. Similarly, Nybakken (1978) and Potts (1970) found individuals of the dorid opisthobranchs *Triopha maculata* MacFarland, 1905 and *Onchidoris bilamellata* (L., 1767) (Müller, 1776 as *O. fusca*) under rocks in winter, suggesting that the sudden appearance of certain species on the shore can be explained by a change in their behaviour from cryptic under-rock habits to actively feeding on surface habitation when hydrodynamic conditions change. A similar conclusion was reported by Trowbridge (1992) for adult individuals of the common sacoglossan *Placida dendritica* (Alder & Hancock, 1843). In winter, when strong hydrodynamism levels occur, *P. dendritica* moves from wave-exposed to wave-protected thalli of *Codium setchellii* Gardner, 1919.

In conclusion, this short-term study (~1 yr) seems to support the hypothesis that occasionally (i.e. in March) *O. olivacea* prefers a cryptic under-rock habitat instead of non-cryptic habitats such as blocks, and therefore supports the idea that the density of this species is not highly variable *per se* (Thibaut & Meinesz 2000; Gianguzza et al. 2007). Future work is needed to further investigate temporal fluctuations of this species over appropriate temporal and spatial scales. Perhaps one profitable approach would be to consider field experiments to test micro-habitat selection, in conjunction with more specific environmental factors, such as hydrodynamics and temperature. Also, considering the behaviour of *O. olivacea* in the presence of its ancestral food (*C. prolifera*) would be important to evaluate the importance of intrinsic factors in modulating the behavior of this slug. This would be important to better understand the dynamics of abundance of sacoglossan sea slugs, traditionally thought of as unpredictable (Clark 1994).

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