

Insights into ecological and reproductive aspects of two cryptogenic peracarid crustaceans of the Argentinian coast

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ABSTRACT

Peracarid crustaceans belong to the most important agglomerating macrofauna in sedimentary habitats. The amphipod *Monocorophium insidiosum* CRAWFORD, 1937 and the tanaid *Tanais dulongii* AUDOUIN, 1926 are listed as invasive species. In the present study, we investigated the ecology of *M. insidiosum* and *T. aff. dulongii* from the Argentinian coast. Both crustaceans were breeding under laboratory conditions to study their fecundity and growth. Additionally their behavior and potential interspecific relations have been investigated in four different laboratory experiments. We evaluated tube building capabilities (experiment 1), and tested gender specific responses of *M. insidiosum* to the presence of empty (experiments 2 and 3), and inhabited *T. aff. dulongii* tubes (experiment 4). Our results showed high fecundity (three generations within four weeks) and growth rates (duplication of body lengths in two weeks) for *M. insidiosum*. Two tube construction strategies were distinguished: a tube changing behavior for the amphipod *M. insidiosum*, showing greater construction activity for females, and tube keeping behavior for *T. aff. dulongii*. Overall, tanaid tubes were frequently claimed by *M. insidiosum*, demonstrating a close interspecific relationship and resulting in decreased sediment aggregating activity. In the light of our observations it may be affirmed that these invasive species are probably frequently distributed along the Patagonian Atlantic coast and will still spread in future.

Descriptors: *Monocorophium insidiosum*, *Tanais aff. dulongii*, Amphipods, Epibenthos, North Patagonia, algal-crustacean interactions

RESUMO

Crustáceos da superordem Peracarida formam importantes aglomerados em habitats sedimentares. O anfípode *Monocorophium insidiosum* (CRAWFORD, 1937) e o tanaidáceo *Tanais dulongii* (AUDOUIN, 1926) são classificados como espécies invasoras. No presente estudo, investigamos a ecologia de *M. insidiosum* e de *T. aff. dulongii* na costa argentina. Cultivamos ambos os crustáceos para estudar sua fecundidade e crescimento, e investigamos seu comportamento e potenciais relações interespecíficas em quatro experimentos laboratoriais. Avaliamos a capacidade de construção de tubos (experimento 1) e testamos a reação de machos e fêmeas de *M. insidiosum* em construir tubos na presença de tubos vazios (experimentos 2 e 3) e ocupados (experimento 4) de *T. aff. dulongii*. Nossos resultados mostraram alta fecundidade (três gerações em quatro semanas) e taxa de crescimento (duplicação do comprimento corporal em duas semanas) de *M. insidiosum*. Duas estratégias de construção de tubos foram identificadas: um comportamento de mudança de tubo para *M. insidiosum*, em que fêmeas mostraram maior atividade de construção; e um comportamento de manutenção de tubo para *T. aff. dulongii*. De maneira geral, tubos de tanaidáceos foram frequentemente reivindicados por *M. insidiosum*, demonstrando uma relação interespecífica próxima e resultando numa menor atividade de agregação sedimentar. Segundo nossas observações, é provável que essas espécies invasoras já sejam encontradas ao longo da costa atlântica patagônica, ou que venham a se propagar no futuro.

Descritores: *Monocorophium insidiosum*, *Tanais aff. dulongii*, Anfípodos, Epibenthos, Patagônia do Norte, Interações alga-crustáceo.

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INTRODUCTION

The deposition and stabilization of sediments play a crucial role in the coastal ecosystem, affecting the deposit feeding fauna and impacting the physiology of phototrophic organisms due to changes in the underwater light regimes (SCHIEL et al., 2006). Particle budgets of estuary and coastal zones are highly dependent on the degree to which particles passing the benthic boundary layer and to which they are incorporated and stabilized against resuspension and erosion (DYER, 1995). Peracarid crustaceans are the most important sediment agglomerating macrofauna in sedimentary habitats (CONLAN, 1994; and MOURITSEN et al., 1998). Due to their high abundances and extensive building activities, these crustaceans are suspected of altering the sediment properties (e.g. granulometric and hydrodynamic) of their environment (KRASNOW and TAGHON, 1997). Observational studies clearly evidenced selective particle sorting activities of tanaids and amphipods, with a close sorting activities feeding and tube construction activities (MENDOZA, 1982; MILLER, 1984; KRASNOW and TAGHON, 1997). Particles grasped by the chelipeds are sorted in the maxillipeds and either moved to the mouth or to the pereopods, where specialized glands produce a mucous thread (JOHNSON and ATTRAMADAL, 1982) which is used by the animals to agglomerate their burrows (KRASNOW and TAGHON, 1997; KRONENBERGER et al., 2012a, b). Overall the composition of peracarid burrows (tubes) depends on different factors, such as species identity, animal size, and the presence of particle associated microbes (ULRICH et al., 1995; DIXON and MOORE, 1997; KRASNOW and TAGHON, 1997). Due to their important role in substrate modification, peracarid crustaceans play a crucial role for benthic-pelagic coupling (NICKEL, 2004). The place of nest construction is vital for peracarid crustaceans and has been shown to be associated with different macroalgae (GUERA-GARCÍA et al., 2009; CERDA et al., 2010). Nest-building peracarid crustaceans are usually in high numbers above macroalgae, forming assemblages of different crustacean species (GUERA-GARCÍA et al., 2009). These assemblages are of interest to a variety of marine predators (JARQUIN-GONZÁLEZ; GARCÍA-MADRIGAL, 2010), including commercially important fish species (YAMAMOTO; TOMINAGA, 2005), shore birds (JAZDZWESKI; KONOPACKA, 1999) and marine mammals (BURNS et al., 1998).

At our study site in San Antonio Bay (40°43'S, 64°56'W), *Monocorophium insidiosum* (CRAWFORD, 1937) was frequently observed intermixed with the tanaid *Tanais* aff. *dulongii* (Audouin, 1926), forming assemblages on different macroalgae (*Polysiphonia* sp., *Ulva lactuca*, *Corallina officinalis*, *Punctaria* sp.). Due to their high tolerance and adaptation potential under changing environmental conditions, these peracarid crustaceans are listed as invasive species worldwide (FOFONOFF et al., 2003). They are known to be disseminated by shipping (MINCHIN, 2007) and aquaculture activities (GROSHOLZ et al., 2012), which have transported them to many coastal systems worldwide (KEVREKIDIS, 2004; WINFIELD et al., 2011). Both species are commonly found along the Argentinian coast (ADAMI, 2008; ALABANO et al., 2006, 2009; GUTIÉRREZ et al., 2000; VALLARINO et al., 2002; RIVERO et al., 2005; SUEIRO et al., 2011, 2012). *M. insidiosum* is found to range from Ushuaia (54°48' S, 68°18' W) (Schellenberg 1931) to Bahía de Samborom (35°47'S, 57°22'W) (ALONSO DE PINA, 1997) as is *T. dulongii* from Puerto Madryn (42° 46' S, 65° 2' W) (GIAMBIAGI, 1922, 1923) to Mar del Plata (37° 59'S, 57° 34' W) (RUMBOLD et al., 2012). Despite their ecological importance and observed high abundance little is known about the distribution and ecology of *M. insidiosum* and *T. aff. dulongii* on the Argentinian coast.

In order to study crustacean ecology and investigate its potential impact on the coastal system this study: 1) investigated the abundance of these species within a tidal channel system on the North Patagonian coast (San Antonio Bay: 40°43'S, 64°56'W) in relation to autochthonous macroalgal communities; 2) studied crustacean fecundity and growth and 3) tested crustacean behaviour and potential interspecific relations *in vitro*, by studying tube building capabilities and gender specific responses of *M. insidiosum* to the presence of empty and inhabited *T. aff. dulongii* tubes.

MATERIAL AND METHODS

STUDY AREA

San Antonio Bay is a semi-enclosed bay of 80 km² on the northern Patagonian Atlantic coast (Figure 1A), characterized by the extensive intertidal alterations (symmetric macrotidal regime up to 9 m). Within the area a tidal channel (40°43'37.50"S, 64°56'48.30"W) runs parallel to the coast without direct contact to populated areas. The benthic environment at the research site consists of mixed

sediment substrate, including cobbles, pebbles, mussel and snail shells, on which sessile invertebrates, diatoms and macroalgae grow attached.

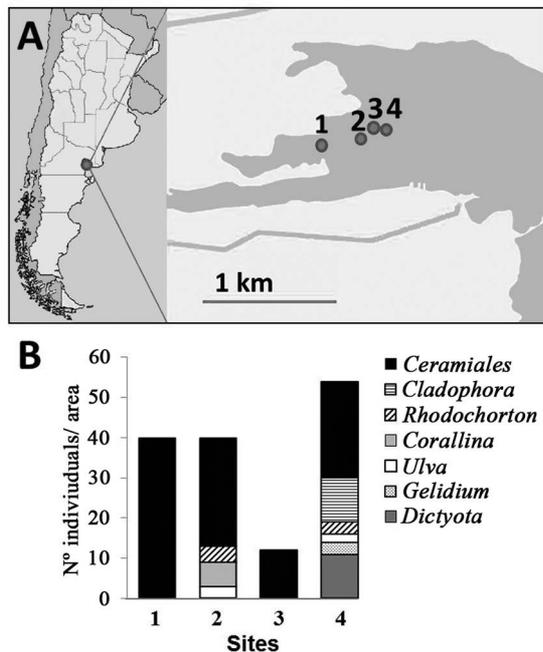


Figure 1. A) Position of sampling sites (1-4) within the Bay of San Antonio (Argentina; S40°43' W64°56'); B) Variations in macroalgae composition and abundances (individual taxa number number/300 cm²) at the different sampling sites.

MACROALGAL-CRUSTACEAN FIELD SURVEYS

The distribution and abundance of *M. insidiosum* and *T. aff. dulongii* in relation to different macroalgae (objective 1) had been observed during surveys undertaken in January 2012. We evaluated the abundance of macroalgae in terms of percentage cover, using photo quadrats (50 cm x 50 cm, n = 4) at four different sites along the tidal channel (Figure 1B). From each photo quadrat a picture was taken and analyzed for percentage cover using the CPCe V 4.1 (Coral Point Count with Excel extensions) software program (KÖHLER and GILL, 2006), which estimates percentage cover of different taxa applied to a grid of 100 points in the digital photographs (KÖHLER and GILL, 2006). At each site an area of 300 cm² was subsampled for all the macroalgae present. The macroalgae sampled were transported in plastic bags and preserved on herbarsheets without any prior cleaning procedures. The invertebrates in the transport bags were preserved separately in formalized seawater (4% Formol). Invertebrate and algal samples

were transferred to the laboratory and investigated, using stereomicroscope (Nikon SMZ 1500) and microscope (4x to 100x magnification; Nikon Eclipse 80i). Herbar material was remoistened prior to identification, scanned for crustacean presence and macroalgae were identified to the lowest possible taxonomic level. Additional formalized crustaceans were transferred to filtrated seawater (5 µm mesh) prior to investigation.

CULTURING CONDITIONS

Individuals of *Ulva lactuca* LINNAEUS (1753) and *Polysiphonia* sp., identified as substrate for peracarid crustaceans, were sampled together with their associated fauna in the research area in February and October 2013. Field material was transferred under cooled (approximately 4° C) and aerated conditions to laboratory facilities. In the laboratory mixed material was transferred to an aerated aquarium (10 x 20 x 40 cm) filled with filtrated seawater (< 30 µm) taken from the area (35% salinity) until experimental start. Cultivation conditions were kept constant, at a temperature of 19 °C, subdued light (~15 µmol m⁻² s⁻¹ PAR) and a 12/12 h photoperiod.

FECUNDITY AND GROWTH OF *T. AFF. DULONGII* AND *M. INSIDIOSUM*

In order to study the reproduction and growth of both crustaceans (objective 2), three oviparous females of *M. insidiosum* and *T. aff. dulongii* respectively were chosen and isolated in dishes of 200 ml, individually equipped with filtered seawater (filtrated 30 µm), sediment diluted in seawater (transferred with a 2 ml pipette) and algal fragments (see below) taken from the research area. The incubations were performed under aerated conditions, the water was changed (50%) and sediment (2 ml) aggregated weekly, for a period of four weeks. Crustacean juveniles and numbers of tubes were noted and sizes were measured weekly, using a stereomicroscope (Nikon SMZ 1500; 1x - 3x magnification). The experimental lasted a month.

CRUSTACEAN BEHAVIOUR *IN VITRO*

To study both tube housing behavior and potential species interactions (objective 3), a series of four different experiments were run during summer 2013 (February experiment 1 and 2), and spring 2013 (October experiment 3 and 4). The experimental scheme of all the experiments is presented in Figure 2.

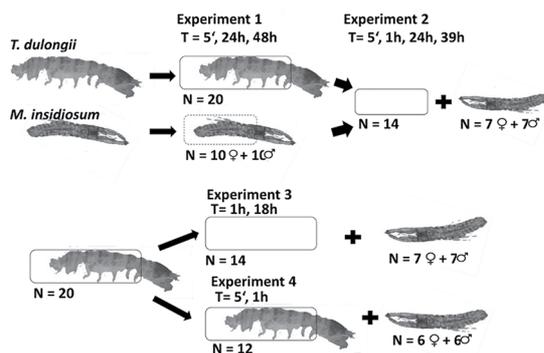


Figure 2. Overview of four different experiments testing for intraspecific interactions between *Monocorophium insidiosum* and *Tanais* aff. *dulongii*. Experimental times (T) and replication numbers (N) are given to each experiment.

Prior to each experiment, crustaceans were transferred individually to a prepared petri dish ($d = 6$ cm). Each petri dish was filled with 10 ml of seawater (filtered, $30 \mu\text{m}$) taken from the area. To provide different material for tube constructions, common macroalgae (1.5 - 2 cm thallus) from the area were added (experiments 1-2: *Ulva lactuca* and *Polysiphonia* sp., and experiment 3-4: *U. lactuca*, *Polysiphonia* sp. and *Punctaria* sp.). For each dish, two circles ($d = 3$ cm) were cut from *U. lactuca* and *Punctaria* sp. respectively. One of the two circles was cut into five stripes and all the material was added to the petri dish. A piece of *Polysiphonia* thallus (1.5-2 cm length) was added to each dish. In addition, 2 ml of detritus diluted in seawater, transferred with a pipette, was added to each petri dish.

EXPERIMENT 1: TUBE BUILDING CAPABILITIES OF AMPHIPODS AND TANAIDS

For *M. insidiosum*, 10 females and 10 males (~ 1.5 mm body length) were selected. For *T. aff. dulongii*, 20 individuals (~ 3.5 mm body length) were selected randomly, as sexual discrimination caused some difficulty at the beginning of the experiment. Despite this, four egg-carrying females were identified among the individuals chosen. Individuals were placed individually in petri dishes and exposed to starting conditions (see culturing conditions). Tube numbers were registered at three different times, i) right after the start of the experiment (5 min, T0), ii) after a period of 24 hours (T1), and at the end of the experiment, after 48 hours (T2). After T2 all the crustaceans were removed from their tubes. Individual crustacean and tube lengths were measured: body length ratios were calculated. In addition, relative agglomerated sediment area was estimated for active (constructing) crustaceans, as

also: (tube length x tube width)/body length. Petri dishes containing empty tanaid tubes and *M. insidiosum* were selected and transferred to the following experiment.

EXPERIMENT 2-4: RESPONSE OF *M. INSIDIOSUM* TO EMPTY AND INHABITED *T. AFF. DULONGII* TUBES

Experiment 2: Seven males and seven females of *M. insidiosum*, which showed construction activities during experiment 1, were randomly selected. They were individually distributed on petri dishes which contained empty tanaid tubes, filled with fresh sea water and additional construction material. A total of 14 petri dishes were observed at four different times: right after the start of the experiment (5', T0), after 1 hour (T1), after 24 hours (T2), and at the end of the experiment after 39 hours' exposure (T3). At each observational time the individual behavior of *M. insidiosum* was recorded. We distinguished following activities: a) passive: individuals showing no construction activity, b) constructing: individuals agglomerating material, c) housing: individuals within constructed tubes, d) claiming: individuals in claimed tanaid tubes. Moreover, newly constructed amphipod tube numbers were recorded. In order to investigate details of tube construction a tanaid tube occupied by *M. insidiosum* was randomly chosen from experiment 2 and prepared for scanning electronic microscopy following the protocol of PARODI and CAO (2003).

Experiment 3: A total of 20 *T. aff. dulongii* were individually transferred to petri dishes, prepared according to starting conditions. After 20 hours, 15 tanaids had finished their tubes. Constructing tanaids were carefully removed from their tubes and transferred to experiment 4. Petri dishes containing empty tubes were filled with new water and additional construction material. To test the response to the presence of empty tanaid tubes a total of 7 male and 7 female *M. insidiosum* were added individually to each petri dish. Amphipod behavior was observed after 1 (T1) and 18 hours' exposure (T2). In addition newly constructed amphipod tubes were recorded.

Experiment 4: Tanaids from experiment 3 were transferred to petri dishes, prepared according to starting conditions. After 20 hours exposure, 12 of the 13 petri dishes, containing constructing tanaids, were randomly chosen and filled with fresh seawater to oxygenize them. Six male and six female *M. insidiosum* were selected from the field material and were individually distributed to petri dishes containing tanaids within their constructed tubes. Crustacean behavior was observed over the first 5 minutes (T0) and after 1 hour (T1). In addition newly constructed crustacean tube numbers were noted down.

STATISTICAL ANALYSES

Sixteen different statistical analyses, 1- factorial analyses of variances (ANOVA; 1-way ANOVA) and ANOVAs for repeated measurements (Rep. mes. ANOVA) were applied to test for differences between the different factors: experimental time (TIME), male and female individuals (GENDER) and different species (TAXA). We tested for differences in the parameters: i) body lengths, ii) tube numbers, iii) tube lengths, iv) tube/body lengths ratios, v) agglomerated sediments, calculated as tube area (length x width), vi) position of taxa, distinguishing between inside and outside tanaid tubes, vii) individual behavior, distinguishing between tube construction or non-constructing, viii) tube position: distinguishing between close to (< 1 cm distance) or far from a tanaid tube. An overview of all the statistics is presented in Table 1. Homogeneity of variances was tested with Cochran's test and, when necessary, data were arcsine-, fourth-root, or log-transformed to meet homogeneity assumptions. In those cases where transformation did not homogenize the variances, we used Mann-Whitney U-tests (e.g. body length comparisons). Tukey's test of honest significant difference (HSD) was used for *post hoc* comparisons in all cases. Significance levels were set at $p < 0.05$. Statistica 7 software was used for the analyses.

RESULTS

MACROALGAL - CRUSTACEAN ASSOCIATION IN THE STUDY AREA

The research area was mainly covered by macroalgae growing as low patchy tufts (< 5 cm height), attached to pebbles buried in the sediment. The composition of these tuft forming algae varied along the channel (Figure 1B), depending on the present substrates, e.g. *Dictyota dichotoma* was only found attached to bigger stones. Overall the red algal order *Ceramiales* dominated the area, with *Polysiphonia* as the most common genus. *M. insidiosum* and *T. aff. dulongii* were frequently found in the area, often together in the same macroalgae (Figure 3A), mainly on *Ulva lactuca*, *Polysiphonia sp.* and *Corallina officinalis*.

FECUNDITY AND GROWTH

A) *MONOCOROPHIUM INSIDIOSUM*

A high fecundity was observed in *M. insidiosum*, as all three oviparous females bred within the first week and two of the three were observed to be oviparous again, breeding the second generation after a 1-2 week period. One female

was oviparous for the third time at the end of the fourth week. Females were kept together with their hatchlings until the end of the observations. First post-marsupial stages of *M. insidiosum* ($85.3 \pm 11.9 \mu\text{m}$ body length) were observed leaving the mother's tube and starting their tube building activities within the first 20 hours ($168.5 \pm 44.9 \mu\text{m}$ tube length). A slight delay was observed in breeding or in leaving the mother's tube, as a lower number of juveniles were recognized after one (9.4 ± 4.5 individuals) than after two weeks (13.8 ± 2.7 individuals) of breeding. Juveniles showed rapid growth, duplicating their body lengths over the first 2 weeks (Table 1, Figure 4A). After five weeks the first sexual characteristics were observable. Accordingly to body sizes, also a significant growth in tube lengths was observed (Table 1, Figure 4C). The growth in tube sizes was accompanied by frequent rebuilding of tubes (Fig.4E) and a change in construction material from fine mucilaginous detritus to sand grains.

B) *TANAIS AFF. DULONGII*

In contrast to *M. insidiosum*, individuals of *T. aff. dulongii* were scarcely observed outside their tubes. The isolated females seemed to be enclosed in their tubes over breeding time. Only one female presented hatching activity during the period of the experiment. Two weeks after isolation 12 post-marsupial stages ($95.33 \pm 3.93 \mu\text{m}$ body length) were observed leaving the parental tubes (Fig. 4B) and starting constructing tubes ($500 \pm 83.68 \mu\text{m}$ tube lengths). Compared to the adults, the juveniles showed a different type of tube constructions, building long, fine tubes, which seemed to interconnect with each other and agglomerate near the parental tube. Over time these tubes became more condensed (Table 1, Figure 4). No behaviour of tube changing was observed. Material was replaced and tubes were modified as individuals grew. Furthermore, tube protecting behavior was observed towards the end of the study. Comparing the crustacean tubes built by the different adults of *M. insidiosum* and *T. aff. dulongii*, observed in the various experiments a significantly higher tube/body length ratio was observed for *T. aff. dulongii* (Table 1, Figure 4F).

CRUSTACEAN TUBE BUILDING CAPABILITIES (EXPERIMENT 1)

For *M. insidiosum* clear differences were observed in tube constructing behavior as between female and male individuals during the period of the experiment

Table 1. Results of different analyses of variances (ANOVA) applied in the various experiments. Results of Tukey's test are given for each significant comparison.

Nº	Type	Factor	Parameter	ANOVA/Kruskall Wallis	Tukey/Kruskall Wallis
Culturing: Animal and tube growth (Larval stage)					
1. <i>Monocorophium insidiosum</i>					
1	Kruskall-Wallis	TIME	Body length	H3, 106 = 81.49, $p < 0.000$	1 < 2 < 3,4 weeks
2	1-way ANOVA	TIME	Tube length	F3, 118 = 33.44, $p < 0.000$	1 < 2 < 4 weeks
3	Kruskall-Wallis	TIME	Tube number	H3, 14 = 8.84, $p = 0.03$	n.s.
1. <i>Tanais aff. Dulongii</i>					
4	Kruskall-Wallis	TIME	Body length	H2, 19 = 14.90, $p < 0.000$	1 < 3 weeks
5	1-way ANOVA	TIME	Tube length	F2, 26 = 29.59, $p < 0.000$	1 > 2,3 weeks
6	1-way ANOVA	TIME	Tube number	No change observed	
Experiment 1-4: Comparison of <i>M. insidiosum</i> and <i>T. aff. dulongii</i>					
7	Kruskall-Wallis	TAXA	Tube/body ratio	Flog 1,53 = 20.42, $p = 0.000$	<i>T. aff. dulongii</i> > <i>M. insidiosum</i>
Experiment 1: Tube building capacities (Adult stage) of <i>M. insidiosum</i>					
8	1-way ANOVA	GENDER	Body length	F1, 12 = 8.87, $p = 0.01$	Male > Female
9	Rep. mes. ANOVA	GENDER	Agglomerated sediment	T1: F1, 19 = 10.17, $p = 0.005$; T2: n.s.	T1: Female > Male
10	Rep. mes. ANOVA	GENDER	Tube Nº	T1: F1, 19 = 4.56, $p = 0.046$; T2: n.s.	T1: Female > Male
11	Rep. mes. ANOVA	GENDER	Tube length	T1: n.s. T2: n.s.	
12	Rep. mes. ANOVA	GENDER	Tube/Body lengths	T1: n.s. T2: n.s.	
Experiment 2: Effect of tanaid tubes on <i>M. insidiosum</i>					
13	Rep. mes. ANOVA	GENDER	Position	T1: n.s. T2: n.s.	
Experiment 3: Effect of tanaid tubes on <i>M. insidiosum</i>					
14	Rep. mes. ANOVA	GENDER	Position	T1: F1, 13 = 6, $p = 0.03$ T2: n.s.	T1: Male > Female
Experiment 4: Effect of the presence of <i>T. aff. dulongii</i> on <i>M. insidiosum</i>					
15	1-way ANOVA	GENDER	Behavior	F1, 11 = n.s.	
16	1-way ANOVA	GENDER	Tube position	F1, 11 = n.s.	

(Table 1). Despite their smaller body size (3 ± 0.6 mm, Table 1), female amphipods showed a significantly greater tube building activity within the first 24 hours, agglomerating 5.8 ± 1.6 mm² of sediment per mm of body length (~ 16 mm² sediment/day). By contrast only 78% of male individuals had finished their first tube after 24 hours (T1, Figure 5). Male amphipods started to increase their tube building activities by the end of the experiment, whereas females decreased them. In consequence, no differences were found in agglomerated sediment after 48 hours. No gender specific differences were found for tube lengths or tube/body length ratios. Fourteen tanaid tubes were

constructed by *T. aff. dulongii* using detritus and parts of algal material (Figure 3), within the first 24 hours. Fifteen tubes had been constructed, with a maximum of one tube per individual, by the end of the study. Two individuals died during the experiment, the remaining four non-constructing individuals were inactive and showed reduced activity. Compared to the tubes built by *M. insidiosum*, those of *T. aff. dulongii* were constructed with a broader variety of material, including algal fragments and detritus (Figure 3). Closer investigation showed a high microbiological activity, with many filamentous cyanobacteria inhabiting the tube walls (Figure 3E).

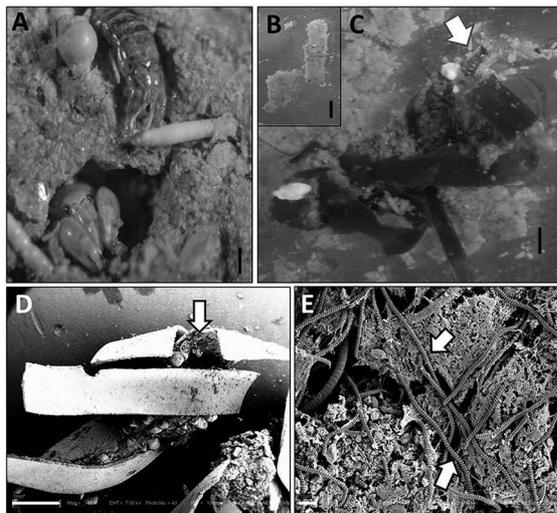


Figure 3. A) Both species housing the same red macroalga *Corallina officinalis* (Linnaeus, 1758). Scale bar = 100 μ m. B) Amphipod tubes built by a female *Monacorophium insidiosum*. Scale bar = 1 mm. C-E) Tanaid tube built by *T. aff. dulongii* with fragments of the macroalga *Ulva lactuca* (Linnaeus, 1753). Arrow indicates position of female *M. insidiosum* housing the tanaid tube during experiment 2. Scale bar = 1 mm. D) Ultrastructure of tanaid tube. Scale bar = 1 mm. Arrow indicates detail of tube wall (E) agglomerated by mucous throat and inhabited by different filamentous cyanobacteria (white arrows). Scale bar = 10 μ m.

RESPONSES OF *M. INSIDIOSUM* TO EMPTY TUBES OF *T. AFF. DULONGII* (EXPERIMENTS 2 AND 3)

In both experiments, a clear tube-claiming behavior was observed. Amphipods started to investigate and claim empty tanaid tubes within the first hour of the experiment. Further, gender-specific differences were registered in experiment 3, in which significantly more males were found in tanaid tubes after the first hour (T1) (Table 1, Figure 6). Interestingly, after 18 hours of experiment these differences vanished, as three male amphipods left the claimed tubes and started to construct their own, while parallel to that the number of claiming females increased over time (Figure 6).

RESPONSE OF *M. INSIDIOSUM* TO THE PRESENCE OF *T. AFF. DULONGII* (EXPERIMENT 4):

Over the first five minutes of exposure to inhabited tanaid tubes, half of the amphipods investigated the substrate of the tanaid tube and three individuals tried to enter the inhabited tubes, but were repelled immediately. After one hour 11 amphipods were found in their own-built tubes. Although no gender-specific differences were statistically identified (Table 1), 80% of the constructing females constructed their tubes at a certain distance (> 1 cm) from the tanaid tubes.

DISCUSSION

In our study, both *M. insidiosum* and *T. aff. dulongii* were frequently found in the intertidal area of San Antonio Bay, on the northern Argentinian Atlantic coast. In general, both crustaceans are considered as typical epibenthic species, constructing their tubes on different natural and artificial substrates (CRAWFORD, 1937; NAIR and ANGER, 1979; KEVREKIDIS, 2004). Their observed common association with different macroalgae might be primarily due to the presence of an elevated, sediment free substrate. Furthermore the observed colonized macroalgal species such as the Rhodophyte *Polysiphonia* sp. hosted a dense epiphytic community composed of diatoms, protozoans and cyanobacteria, which potentially fit into the diet of the studied crustaceans (NAIR and ANGER, 1979; POORE; STOREY, 1999).

As the presence of macroalgae strongly depends on substrate availability (DAVIS, 2009) and shows strong seasonal variations in our research area (MARTINETTO et al., 2010), knowledge of crustacean substrate preferences is crucial to understand the dynamics of crustacean sediment fixation in the area. The observed crustacean-algal interaction might allow us to artificially elevate the sediment agglomeration in the area by providing substrate suitable for algal growth. The observed sediment aggregation activities of the two peracarid crustaceans were considerable. Immediately on leaving their maternal tubes, the post-marsupial stages of *M. insidiosum* and *T. aff. dulongii* started constructing tubes, varying in size and materials used (fine detritus to sediment) according to their crustacean body size.

Comparing the two peracarid crustaceans it was possible to distinguish two different tube-inhabiting strategies: a tube-changing behavior for *M. insidiosum* and a tube-keeping behavior for *T. aff. dulongii*. Constructing and changing its tubes daily, using mainly detritus and sediment components, the behavior of *M. insidiosum* was related to a high sediment agglomeration activity (~ 16 mm² of sediment/day), which consequently led to a high number of empty tubes within a short time. In contrast, *T. aff. dulongii* spent more time on a comparatively bigger tube, which it modifies concisely during its growth, using a variety of different construction materials (e.g. detritus, sediment, algal fragments).

These differences in tube housing were accompanied by different activity patterns - as *T. aff. dulongii*

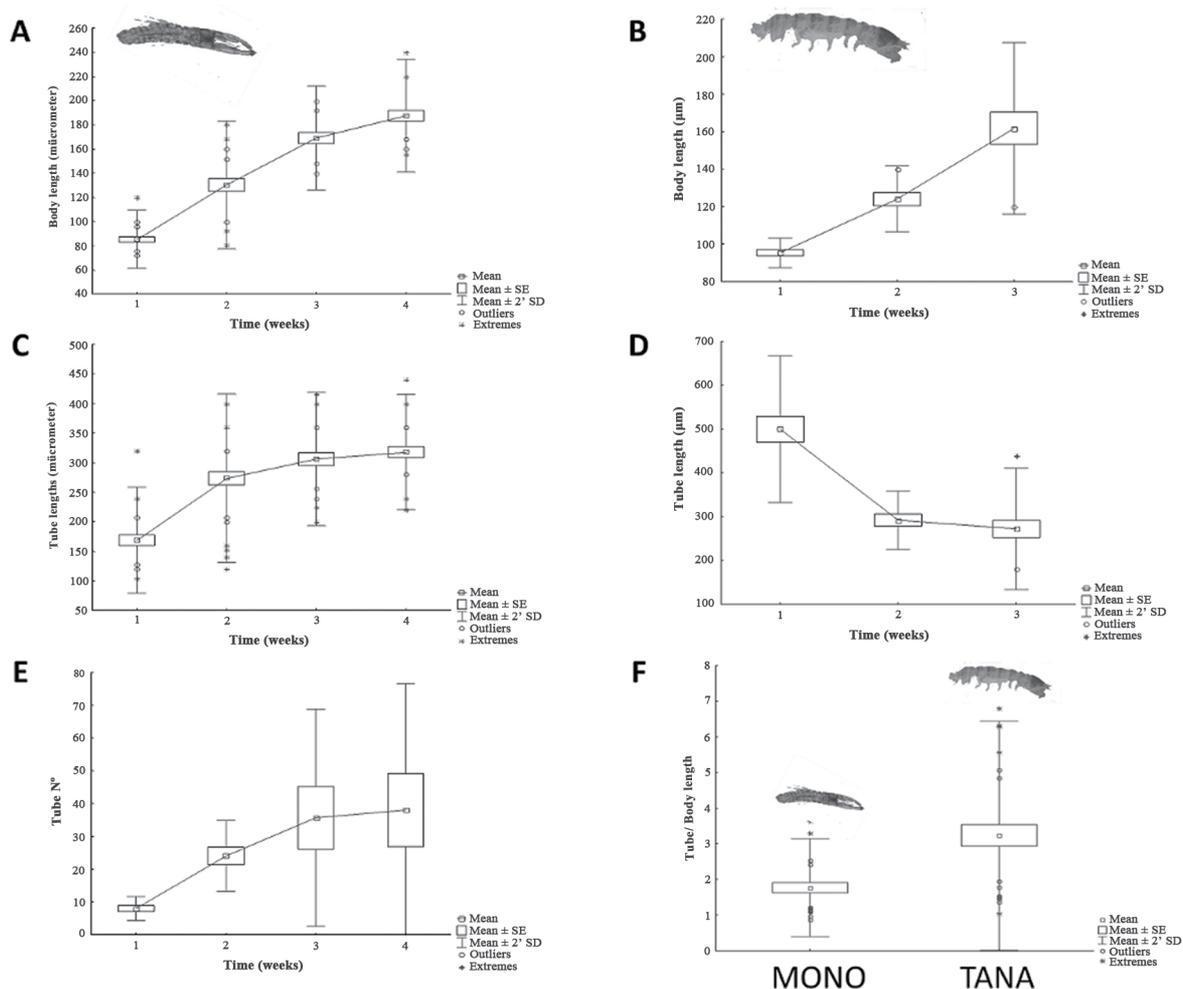


Figure 4. *M. insidiosum* (left) and *T. aff. dulongii* (right). A+B) Growth of juveniles in body lengths and C+D) Changes in tube lengths of juveniles constructed over the first three (*T. aff. dulongii*) and four weeks (*M. insidiosum*) after hatching. E) Increase of tube numbers in juvenile *M. insidiosum* over the first four weeks. F) Comparisons of tube/body length ratio in adult animals.

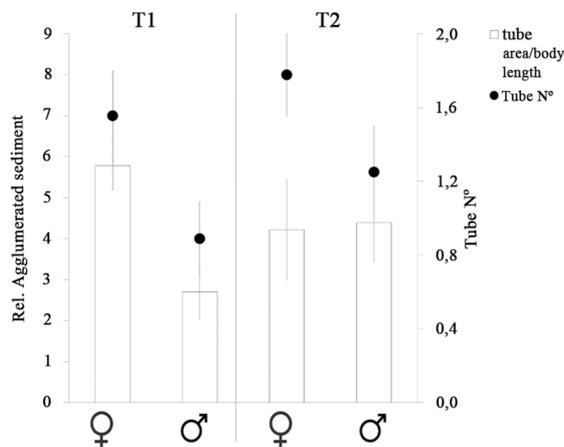


Figure 5. Tube numbers and relative agglomerated sediment of male and female *Monocorophium insidiosum* constructed within 24 hours, measured at two different times (T1 = 24 hours, T2 = 48 hours) in experiment 1.

hardly left its tubes whereas *M. insidiosum* was commonly found outside. The different behavior of *M. insidiosum* corresponded to the precopulatory mating behavior of the *Corophium* genus observed in other studies (CONLAN et al., 1991), whereby male amphipods cruise between the female tubes. Indeed, when removing crustaceans from their tubes, we frequently observed male and female *M. insidiosum* jointly in the same tube. This tube sharing behavior is a common pattern among the Corophidae amphipods, e.g., in *Corophium volutator* (PALLAS, 1766) and might ensure the reproduction success of the cruising male, which guards its mate over a certain time (FORBES et al., 1996). The precopulatory mating activities of *M. insidiosum* might also explain their observed tube-claiming behavior. Interestingly, no gender-specific difference was found.

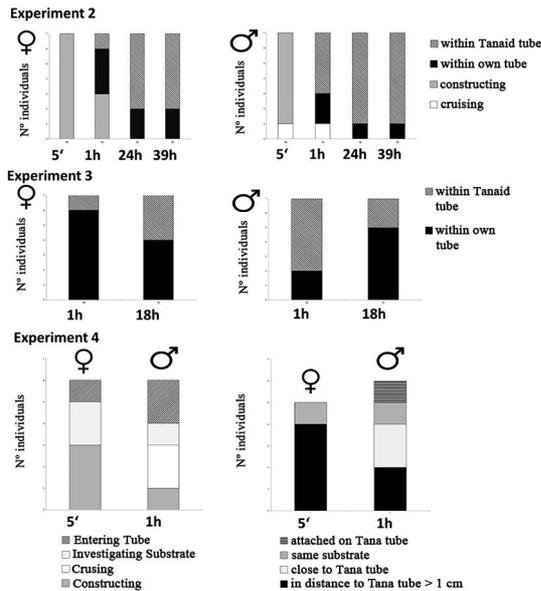


Figure 6. Experiment 2 and 3: Behavioral pattern of *Monocorophium insidiosum* after exposure to empty tanaid tubes over different exposure time (5' to 39h). Experiment 4: Response of *M. insidiosum* to housed tanaid tubes, behavioral observation during first 5 min of exposure (left), and position of amphipod tubes after 1h exposure (right).

The tube-claiming behavior does, in fact, seem to be a common feature in *M. insidiosum*. After the observed claiming of foreign tanaid tubes, it is possible that *M. insidiosum* also claim conspecific tubes, abandoned by individuals during their growth phase. Such intraspecific behavior would strongly affect the dynamics of amphipodal populations and also explain the formation of the dense colonies observed.

The abandoned crustacean tubes might additionally favor other species such as nematodes which were frequently found during the studies gathering in aggregated sediment structures. The tube construction activities are, further, closely connected with foraging behavior in many peracarid crustaceans (MILLER, 1984; KRASNOW; TAGHON, 1997) so the observed differences in crustacean tube building behavior might correspond to different feeding habits. *M. insidiosum* is considered an omnivorous particle feeder (NAIR and ANGER, 1979) which produces pleopod-induced through-tube currents (DIXON and MOORE, 1997). In contrast, tanaids rely more on biofilms than on detritus as a carbon source. They do, in fact, selectively integrate biofilm coated particles in their tubes (KRASNOW; TAGHON, 1997). Indeed, the permanent irrigated inner sites of crustacean tubes provide oxygenated microhabitats of intensive microbial activity, e.g.

bacteria and fungi (ALONGI, 1985). In the present study we also observed a high density of microorganisms (e.g. filamentous cyanobacteria) inhabiting the walls of the tubes constructed by *T. aff. dulongii*. The crustacean tube's associated biofilm might play a crucial role for tanaid females which hardly leave their tubes waiting for "cruising males" and where they enclose themselves during hatching period (BOROWSKY, 1983). This microbial film, provide a potential food source for the breed after leaving the marsupium (Manca stage), which is observed to remain within the maternal tube for about a week (HAMERS and FRANKA, 2000).

Related to the interaction of both crustaceans, the observed tube-claiming behavior of *M. insidiosum* may be indicative of the suitability of tanaid tubes in terms of nourishment for peracarids. The observed behavior is interesting as the resulting reduced tube building activities of *M. insidiosum* might consequently also alter the sediment agglomeration in the adjacent environment. So far it is still unclear under what conditions *T. aff. dulongii* changes its tubes and how far the tube-claiming of *M. insidiosum* may alter the tube-construction behavior of *M. insidiosum* under natural conditions. An alteration in the greater amphipod tube-building activity will not only affect the sedimentary processes but might also have an impact on the associated benthic flora. Macroalgae hosting peracarid crustacean tubes might not only be affected by the presence of sedimentary tubes, but might even profit from the nutrient rich crustacean excretions within the algal thalli. A better knowledge of this and crustacean-algae relations might be crucial for a better understanding of the sedimentation processes in the area.

Overall, due to the observed high fecundity of *M. insidiosum*, the cryptic behavior of *T. aff. dulongii*, the observed high abundances of both crustaceans in the field and frequent records in the recent literature, it is possible that these invasive species are nowadays widely distributed along the Patagonian Atlantic coast. In order to better understand the potential consequences of this for sedimentary habitats along the Patagonian Atlantic coast, further studies on the recent distribution of these potential invaders are urgently required. Our study provides important information on the ecology of the invasive *M. insidiosum* and *T. aff. dulongii* on the North Patagonian coast and gives an insight into the behavioral ecology of the sediment agglomerating crustaceans which will help one to understand and evaluate their observed extension along the northern Patagonian Atlantic coast.

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