

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* on the Argentinian coast. We bred both crustaceans to study their fecundity and growth, and investigated their behavior and potential interspecific relations in four different laboratory experiments. We evaluated tube building capabilities (experiment 1), and tested gender specific responses of *M. insidiosum* to empty (experiments 2 and 3), and housed (*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 *M. insidiosum*, showing greater construction activity on the part of females, and tube keeping behavior on the part of *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 spread still further in the future.

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

RESUMO

Crustáceos da superordem Peracárida pertencem à macrofauna aglomerada mais importante em habitats sedimentares. O anfípodo *Monocorophium insidiosum* (CRAWFORD, 1937) e o tanaidáceo *Tanais dulongii* (AUDOUIN, 1926) são classificados como espécies invasivas. No presente estudo, investigamos a ecologia do *M. insidiosum* e do *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 túneis (experimento 1) e testamos a reação específica de cada sexo do *M. insidiosum* (experimento 4). (**Nenhuma referência a experimentos 2 e 3?**) Nossos resultados mostraram alta fecundidade (três gerações em quatro semanas) e taxa de crescimento (duplicação do comprimento corporal em duas semanas) do *M. insidiosum*. Duas estratégias de construção de túneis foram identificadas: um comportamento de mudança de túnel do *M. insidiosum*, em que fêmeas mostraram maiores atividades de construção; e um comportamento de manutenção de túnel do *T. aff. dulongii*. De maneira geral, túneis 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 invasivas sejam encontradas frequentemente ao longo da costa atlântica patagônica e que elas se propagem 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 on 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 are incorporated and stabilized against resuspension and erosion (DYER, 1995). Peracarid crustaceans are the most important sediment agglomerating macrofauna in sedimentary habitats (CONLAN, 1994; KRASNOW; TAGHON, 1997; MOURITSEN et al., 1998). Due to their high abundances and extensive building activities, these crustaceans are suspected of altering the sediment (e.g. granulometric and hydrodynamic) properties of their environment (KRASNOW; TAGHON, 1997). Observational studies have clearly evidenced a selective particle sorting on the part of tanaids and amphipods, and close relationship between feeding and tube construction (MENDOZA, 1982; MILLER, 1984; KRASNOW; TAGHON, 1997). Thus 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 mucuous thread (JOHNSON; ATTRAMADAL, 1982) which is used by the animals to agglomerate their burrows (KRASNOW; 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; MOORE, 1997; KRASNOW; TAGHON, 1997). Second only to their important role in substrate modification, peracarid crustaceans are crucial in terms of 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 (or, present in greater numbers than?) 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 at (or, of? 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) and 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°79'S) (Schellenberg 1931) to Bahía de Samborom (36°21'S) (ALONSO DE PINA, 1997) as is *T. dulongii* from Puerto Madryn (42°65'S) (GIAMBIAGI, 1922, 1923) to Mar del Plata (38°10'S) (RUMBOLD et al., 2012). Despite their ecological importance and observed high abundance but little is known of 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 frequency 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 under culture conditions, and 3) tested crustacean behaviour and potential interspecific relations *in vitro*, by studying the 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 consequences of a 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 with populated areas. The benthic environment at the research site

consists of mixed sediment substrate, including cobbles, pebbles and mussel and snail shells to which sessile organisms, diatoms and macroalgae grow attached.

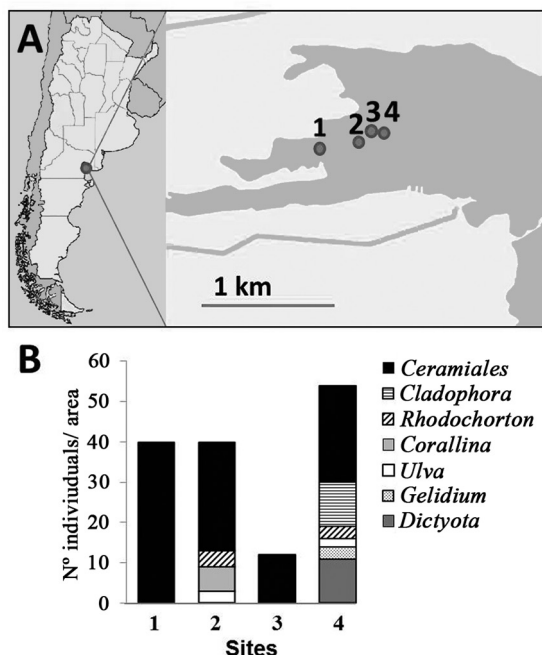


Figure 1. A+B) Position of the tidal channel and sampling sites (1-4) in the Bay of San Antonio (Argentina; S40°43' W64°56'); C) Variations in macroalgae composition and abundances (individual number/300 cm²) at the different sampling sites.

MACROALGAL-CRUSTACEAN SURVEYS (?)

The frequency of *M. insidiosum* and *T. aff. dulongii* in the research area (objective 1) in relation to different macroalgae, was 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; GILL, 2006), which estimates percentage cover of different taxa applied to a grid of 100 points in the digital photographs (KÖHLER; 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 (4* (4x ?) to 100* (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 the laboratory facilities, where the 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 the experiments began 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* from the above-mentioned culture, were isolated in dishes of 200 ml with filtered seawater (30 µm), sediment (2 ml) and algal fragments (see below) taken from the research area. A total of three incubations for each crustacean were performed. The incubations were performed under aerated conditions, the water was changed (50%) and sediment aggregated weekly. Crustacean juveniles and numbers of tubes were noted and sizes were measured weekly, using a stereomicroscope (Nikon SMZ 1500; 1*-3* (1x - 3x ?) magnification). The experimental lasted a month.

CRUSTACEAN BEHAVIOUR *IN VITRO*

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

Prior to each experiment, crustaceans were transferred individually to prepared petri dishes (d = 6 cm). Each petri dish was filled with 10 ml of filtrated seawater (30µm) sampled in the area. To provide different material for tube construction, abundant macroalgae (1.5 - 2 cm thallus) of the area (experiments 1-2: *Ulva lactuca* and *Polysiphonia* sp., and experiment 3-4: *Ulva lactuca*, *Polysiphonia* sp. and *Punctaria* sp.) were added. For each dish, two circles (d = 3 cm) were cut from *U. lactuca* and *Punctaria* sp. respectively. One circle of each thallus was cut into five stripes and all the material was added to the petri dish. A piece of *Polysiphonia* thallus (1.5-2 cm) was, further, added to each dish. In addition, 2 ml of detritus diluted in seawater, soaked (?) with a pipette, was added to each petri dish.

EXPERIMENT 1: TUBE BUILDING CAPABILITIES OF AMPHIPODS AND TANAIIDS

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 exercised construction activity during experiment 1, were randomly selected. They were individually distributed on petri dishes which contained empty tanaid tubes, filled with fresh sea new 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). The individual behavior of *M. insidiosum* was recorded at different times. We distinguished the 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. Next to (quer dizer, ao lado de? ou As well as?) activities, newly constructed amphipod tube numbers were recorded. In order to investigate construction details, a tanaid tube occupied by *M. insidiosum* was randomly chosen from experiment 2 and prepared for scanning electronic microscopic analyses (ou, analysis?), in accordance with the protocol of PARODI & CAO (2003).

Experiment 3: A total of 20 *T. aff. dulongii* were 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 tube numbers 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 field material and individually distributed to petri dishes containing tanaids in 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 AREA

The research site 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 substrate present, e.g. *Dictyota dichotoma* was only found attached to bigger stones. 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 2A), mainly on *Ulva lactuca*, *Polysiphonia sp.* and *Corallina officinalis*.

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

A) *MONOCOROPHIUM INSIDIOSUM*

A higher fecundity were observed, as all three oviparous females bred within the first week of culturing and two of the three were observed to be oviparous again, breeding the second generation after a 1-2 week period. One female was seen to be oviparous for the third time by 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 ± 11.9 μm body length) were observed leaving the mother's tube and starting their tube building activities within the first 20 hours (168.5 ± 44.9 μm tube length). A slight delay was observed in breeding or in leaving the mother's tube, as a

lower number of juveniles were recognized one (9.4 ± 4.5 individuals) than two weeks (13.8 ± 2.7 individuals) after breeding. Juveniles showed significant growth rates, duplicating their body lengths over the first 2 weeks (Table 1, Figure 4). After five weeks the first sexual characteristics were observable. Accordingly to body size, also a significant growth in tube lengths was observed (Table 1, Figure 4). The growth in tube sizes was accompanied by frequent rebuilding of tubes and a change in construction material from fine mucilaginous detritus to sand grains at later stages.

B) *TANAIS AFF. DULONGII*

In contrast to *M. insidiosum*, individuals of *T. aff. dulongii* were scarcely ever observed outside their tubes. The isolated females seemed to be enclosed in their tubes during breeding activity. Only one female presented hatching activity during the period of the experiment. Two weeks after isolation 12 post-marsupial stages (95.33 ± 3.93 μm body length) were observed leaving the parental tubes and starting constructing tubes (500 ± 83.68 μm tube lengths). A different method of tube construction was observed for the juveniles, these organisms beginning the construction of 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 tube change behavior (**change in tube behavior, tube changing behavior?**) 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 adult *M. insidiosum* and *T. aff. dulongii* observed in the various experiments showed a significantly higher tube/body length ratio 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). 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 mm^2 of sediment per mm of body length (~ 16 mm^2 sediment/day). By contrast only 78% of male individuals had finished their first tube after 24 hours (T1). 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 2L), within the first 24 hours (Figure 5). 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 only reduced their activity. Compared to tubes built by (?) *M. insidiosum*, those of *T. aff. dulongii* were constructed of a broader variety of material, including algal fragments and detritus (Figure 2J-L). Closer investigation shows great microbiological activity, with many filamentous cyanobacteria inhabiting the tube walls (Figure 2L).

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 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 typical epibenthic species, constructing their tubes on different natural and artificial substrates (CRAWFORD, 1937; NAIR; ANGER, 1979; KEVREKIDIS, 2004). Their observed common association with different macroalgae might be primarily due to the presence of an elevated, sediment free substrate. Further, 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 crustaceans investigated (NAIR; ANGER, 1979; POORE; STOREY, 1999).

As the presence of macroalgae depends greatly on substrate qualities (DAVIS, 2009) and shows strong seasonal variations in our research area (MARTINETTO et al., 2010), knowledge of crustacean substrate preferences is crucial to understanding the dynamics of the crustacean sedimentation fixation of the area. The observed crustacean-algal interaction enabled us to 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 great sediment agglomeration activity (~ 16 mm² of sediment/day) and 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* was hardly ever observed outside its tubes whereas *M. insidiosum* was commonly found outside its tubes, showing strong gender-specific differences. 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.

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 favor other species such as nematodes which were frequently found during the studies gathering in aggregated sediment structures, too. 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. Thus *M. insidiosum* is considered an omnivorous particle feeder (NAIR; ANGER, 1979) which produces pleopod-induced through-tube currents (DIXON; 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, which is a potential food source for the breed after leaving the marsupium (Manca stage), is observed to remain within the maternal tube for about a week (HAMERS; 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-alga 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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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>M. 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>T. 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.	

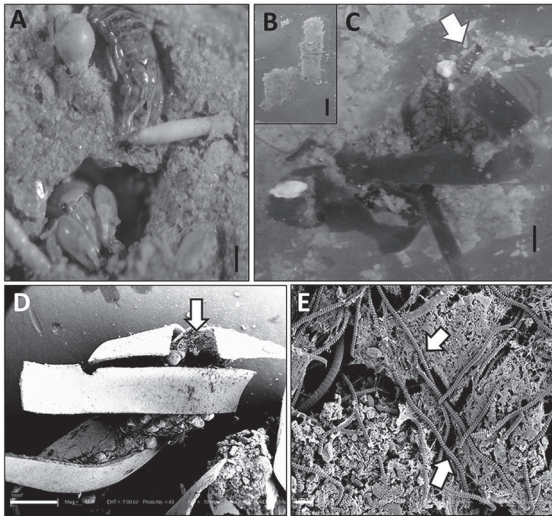


Figure 2. A) Both species housing the same red macroalga *Corallina officinalis* (Linnaeus, 1758). Scale bar = 100 μ m. B) Amphipod tubes built by a female *M. insidiosum*. Scale bar = 1 mm. C-E) Tanaid tube built by *T. aff. dulongii* with fragments of the macroalga *Ulva lactuca* (Linnaeus, 1753). 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 threat and inhabited by different filamentous cyanobacteria (white arrows). Scale bar = 10 μ m.

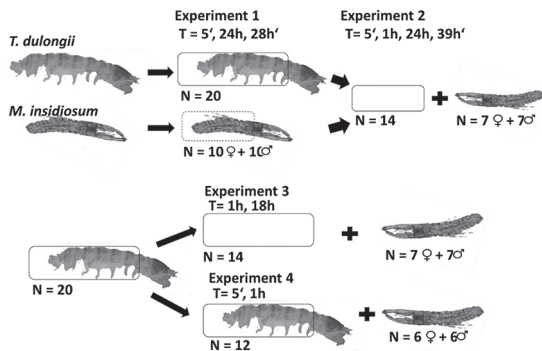


Figure 3. Overview of four different experiments testing for intraspecific interactions between *Monocorophium insidiosum* and *Tanais aff. dulongii*. Experimental times (T) and replication numbers (N) are given to each experiment.

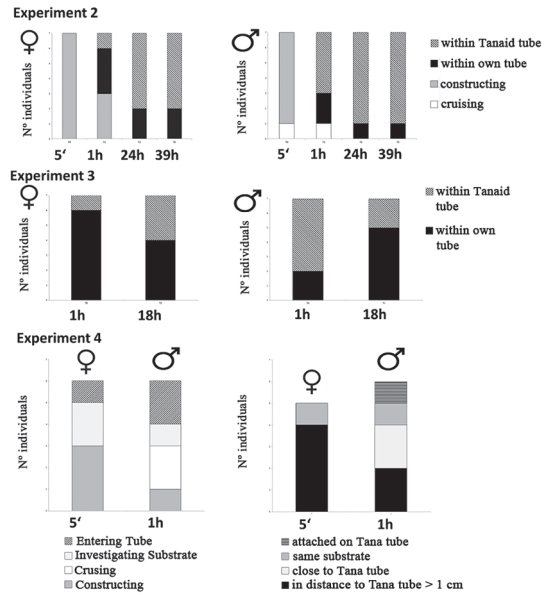


Figure 6. Experiment 2 and 3: Behavioral pattern of *M. insidiosum* after exposure to empty tanaid tubes over different exposure time (5' to 39h). Experiment 4: Response of *M. insidiosum* to housed tanaid tubes, behavioral observation during first 5 min of exposure (left), and position of amphipod tubes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

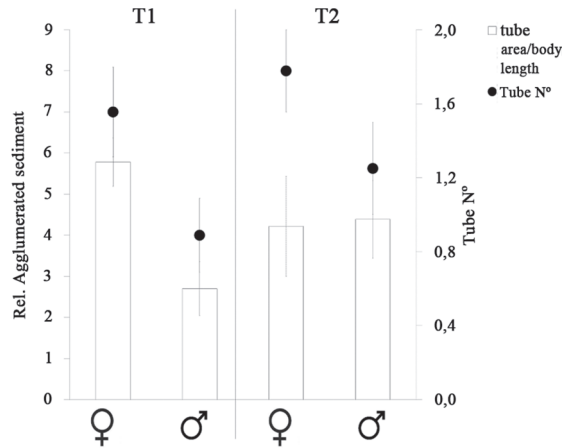


Figure 5. Tube numbers and relative agglomerated sediment of male and female *M. insidiosum* constructed within 24 hours, measured at two different times (T1 = 24 hours, T2 = 48 hours) in experiment 1.

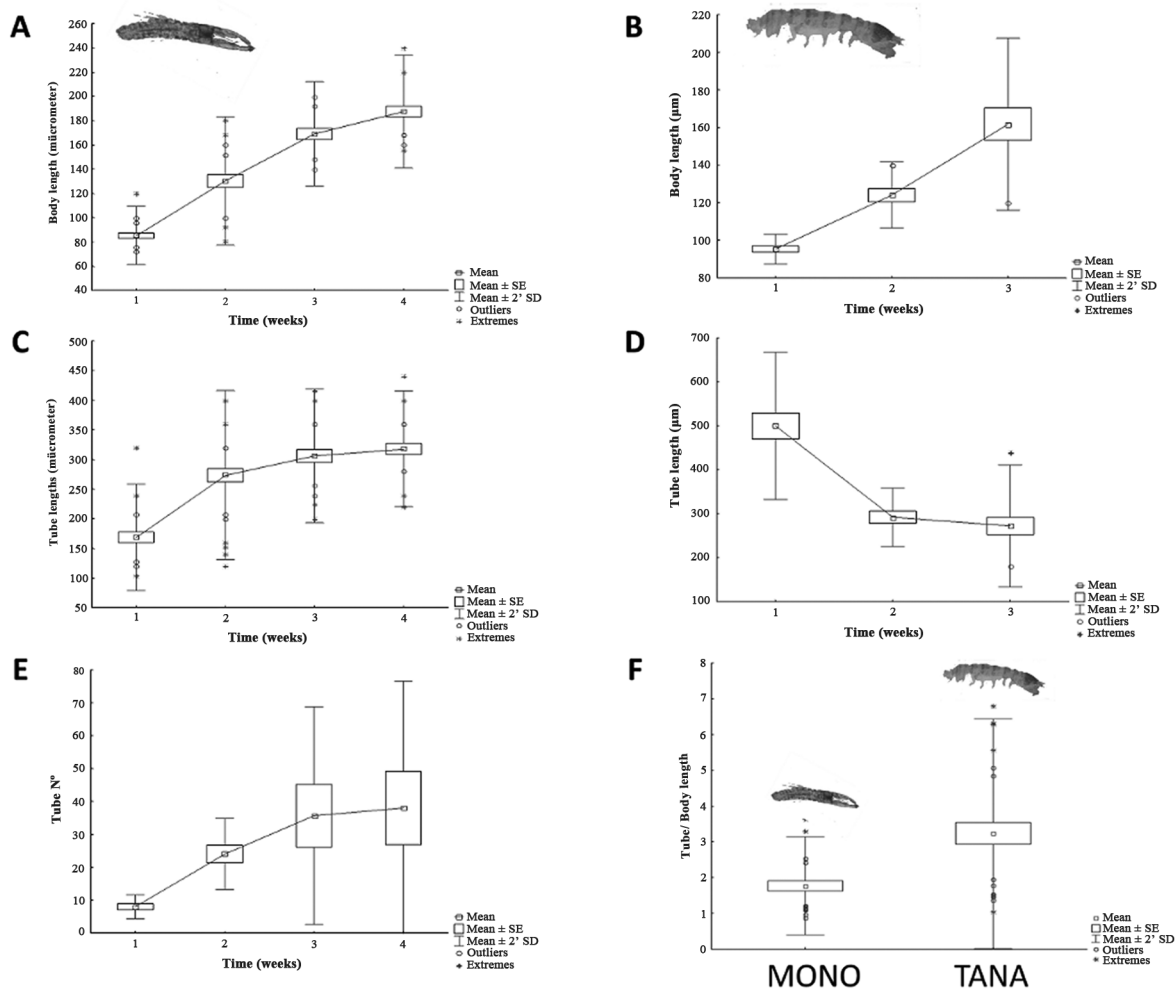


Figure 4. *M. insidiosum* (left) and *T. aff. dulongii* (right). A+B) Growth of juveniles in body lengths and C+D) Changes in tube lengths of juveniles constructed over the first three (*T. aff. dulongii*) and four weeks (*M. insidiosum*) after hatching. E) Increase of tube numbers in juvenile *M. insidiosum*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