# *How to link a burrow to its inhabitant*
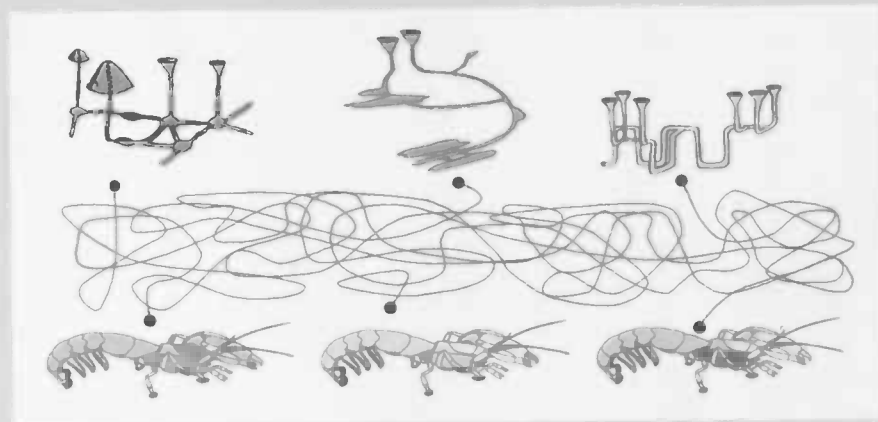
## *A classification model for thalassinidean shrimps using the morphology of their burrows*

**Karin Troost**
*July 2001*
**Department of Marine Biology**
**State University of Groningen**
*Supervisor:* **Dr. Eize J. Stamhuis**

# *How to link a burrow to its inhabitant*

*A classification model for thalassinidean shrimps
using the morphology of their burrows*

**Karin Troost**
*July 2001*
**Department of Marine Biology**
**State University of Groningen**
*Supervisor:* **Dr. Eize J. Stamhuis**

## Summary

Thalassinidean shrimps are common burrowers in marine and estuarine sediments. Their burrows can vary from simple to very complex and from a few centimetres to a few metres in depth. These shrimps are thought to deposit feed, to filter feed and to scavenge or even cultivate micro-organisms on organic debris for consumption, depending on the species that is dealt with. It is generally believed that the morphology of a burrow reflects the feeding strategy of the inhabitant shrimp. With that in mind, a few models have been constructed in the past that classified the shrimps into trophic categories using the morphology of their burrows.

Although a large variety of burrow systems is known nowadays thanks to the relatively new resin casting technique, few is known about the inhabiting animals since they often manage to escape before the researchers have even laid their eyes on these elusive animals. In this thesis, a model is presented that not only classifies the shrimps into trophic categories, but that also makes it possible to identify a shrimp without even having to look at the animal itself. Like in the earlier models, shrimps were classified according to their burrow characteristics. This time, however, the classification was based on a cluster analysis in stead of assumptions regarding the importance of different characteristics. Therefore, the model presented here is believed to be less biased than the earlier models and because of that, more reliable.

## Samenvatting

Kreeftjes behorend tot de thalassinidea komen veel voor in mariene en estuariene sedimenten waarin ze hun burchten graven. Deze burchten kunnen variëren van eenvoudig tot zeer complex en van enkele centimeters tot enkele meters diep. Ze oefenen verschillende voedingsstrategieën uit, zoals "deposit feeding", "filter feeding" en ook wordt aangenomen dat ze aaseters zijn van organisch materiaal waar ze mogelijk ook micro-organismen op kweken voor consumptie. De voedingsstrategie verschilt waarschijnlijk per soort. Over het algemeen wordt aangenomen dat de morfologie van hun burchten hun voedingsmechanisme weerspiegelt. Met dit in gedachten, zijn recentelijk een aantal modellen geconstrueerd die alle soorten indelen in een aantal categorien met betrekking tot hun voedselmechanisme, aan de hand van hun burchtmorfologieën.

Hoewel vooral de laatste jaren veel meer bekend is geworden over de burchten van de gangen-gravende kreeftjes, dankzij vrij nieuw methoden voor het maken van afgietsels, is er erg weinig bekend over het beestje zelf. Dit komt doordat ze vaak al ontsnapt zijn voordat een onderzoeker ze zelfs maar heeft kunnen bekijken. In deze scriptie wordt een model gepresenteerd dat, naast het indelen van de soorten in trofische groepen, het mogelijk maakt om een soort te identificeren zonder naar het beestje zelf te hoeven kijken. Determinatie zal dankzij dit model volledig gedaan kunnen worden aan de hand van de burchtmorfologie. Net als in de voorafgaande modellen werden burchtkenmerken gebruikt om tot een indeling te komen. De indeling die in deze scriptie wordt gepresenteerd zal echter minder bevooroordeeld zijn dan in de vorige modellen omdat de indeling berust op een clusteranalyse in plaats van op aannames betreffende welke kenmerken belangrijk zijn. Daarom zal dit nieuwe model betrouwbaarder zijn dan de voorafgaande.

# Table of contents

## Introduction

### Thalassinidean shrimps

Thalassinidean shrimps are among the most common bioturbators in marine and estuarine sediments (33, 9, 21, 65, 22). Their entire life is spent inside their burrows, except for a larval phase which may be pelagic (18, 22). These burrows can be up to 2.5 metres deep (39) and very complex (34). Until now, a large variety of burrow types is known thanks to relatively new resin casting techniques (52, 16, 45, 3). Before, the burrow tunnels could be traced by use of willow branches or rubber tubing (54, 43) or by meticuously digging out the burrow (54, 10). The resin casting technique has rendered a lot of burrow casts of different species (18, 39, 34, 40, 51, 35, 70, 5). But except in those cases where the resident animal was trapped in the resin (21) or extracted from the burrow with a suction pump (30, see: 6) or by air-lifting (55) before the burrow was cast, the inhabitant shrimps were often able to escape quite easily before their identity could be determined. So it was not always certain which species a burrow belonged to (52, 16, 8, 39).
Using the model presented in this thesis, it will be possible to identify a shrimp without even having to look at the animal itself, as long as its burrow morphology is known.

### Thalassinidean burrows

Thalassinidean burrows are found in a great variety of forms. Some are very simple, extending to no more than ten centimetres into the sediment whereas others are very complex and may extend to a depth of about two metres into the sediment. A short overview of burrow types and terminology, largely based on Nickell & Atkinson (35), will be given in this section.
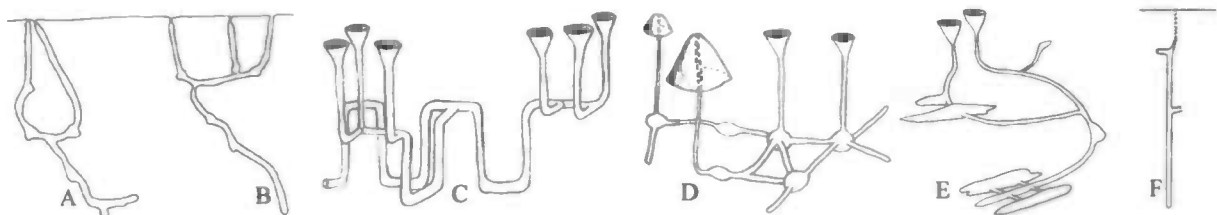


Figure 1: All five burrow types. 1A: simple U/Y burrow (*U pusilla*, 12), 1B: simple U/Y burrow with a second U (*U pusilla*, 12), 1C: multiple U burrow (*Calocaris macandreae*, after 34), 1D: lattice burrow (*C subterranea*, after 53) complete with mounds at the exhalant openings at funnel-shaped inhalant openings, 1E: spiralling main tunnel (*Jaxea nocturna*, after 40), 1F: single shaft burrow (*C major*, 43).

A very common burrow type is the 'simple U or Y' burrow (fig. **1a**). It exists of a U-shaped section with in most cases an additional shaft extending further into the sediment from the lowest part of the U (38, 12, 32, 1, 35). In some cases, a shaft from the lowest part of the U will extend horizontally and then vertically towards the surface, forming a second U (fig. **1b**) (12). These simple U/Y burrows will have 2 to 3 openings to the surface and are commonly assigned to the Upogebiidae as a group (12, 13, 22, 35, 2). When more U-shaped sections are formed, it is called a 'multiple U' burrow (fig. **1c**) (34, 51). A more complex burrow type is the 'lattice burrow' (fig. **1d**) (10, 69, 49, 53). Such a burrow consists of a lattice of galleries and tunnels, with 1 to 8 openings to the surface. One shaft is usually narrower than the other shafts and has an exhalant function. Water is pumped out of the burrow by the beating of the shrimp's pleopods via the exhalant opening. Not uncommonly, a sediment mound can be found surrounding the opening of such an exhalant shaft to the surface. A sediment mound can however also be found at the openings of other burrow types (1, 70). The other shafts have an inhalant function (49, 53). An inhalant opening is often funnel-shaped, probably due to erosion of the sediment by the water current (49) although Dworschak (13) considered a funnel-shaped opening to be a trap for debris. According to Atkinson & Nash (4) a funnel-shaped opening exists when the edge of a thistle-shaped opening, that was formed when the animal somersaulted near the surface in order to turn, collapses.

Some burrows only have one opening to the surface (fig. **1e**) (43, 39). Basically, they exist of one vertical shaft, with or without branching in the deepest section of the burrow. In this thesis such burrows will be called 'single shaft' burrows. Finally, there are those burrows that consist of one or two gently spiralling main tunnels (fig **1f**) (40, 35). In cases where there are two main tunnels, they will join deeper in the sediment to form one main tunnel. It is assumed that these tunnels spiral up to the surface because of the inhabitant's bulldozing activities.

## Feeding

In thalassinidean feeding, three main mechanisms are usually recognized: deposit feeding, filter feeding and scavenging. Deposit feeders generally build burrows that have a complex morphology. These highly branched burrow systems are constantly changing because of the inhabitants active burrowing in search for new sediment layers that are rich in organic matter. They process large volumes of sediment that are expelled daily via the narrow exhalant shaft and that is deposited around the exhalant opening in the shape of a large volcanoe-like mound. Also large chambers have been associated with this feeding mechanism (56, 35, 53).

Filter feeders generally build simple, permanent U- or Y-shaped burrows. Such burrows are believed to be adapted for feeding by the efficient circulation of water through it. The shrimps pump water through their burrows by actively beating their pleopods. The generated current is consequently sieved through the shrimp's setal basket. Upogebiids are commonly assigned to this trophic group (12, 13, 22, 35, 2). For the third trophic category, many names have been mentioned like 'seagrass-/algae-harvesters' (56), 'drift catchers' (22) and 'omnivorous scavengers' (63). Probably the fact that little is know about this feeding mechanism gave rise to the variety in names. These shrimps have been observed to actively introduce seagrass or other algal material into their burrows that was consequently stored in deep chambers or worked into the burrow wall. They are thought to feed on the organic debris or even on micro-organisms, cultivated on the organic matter. Their burrows are assumed to be deep, rather simple and lacking a sediment mound at the surface (34, 56, 35).

## Earlier classification models

Earlier classification models have been made by De Vaugelas (63), Griffis & Suchanek (22) and Nickell & Atkinson (35).
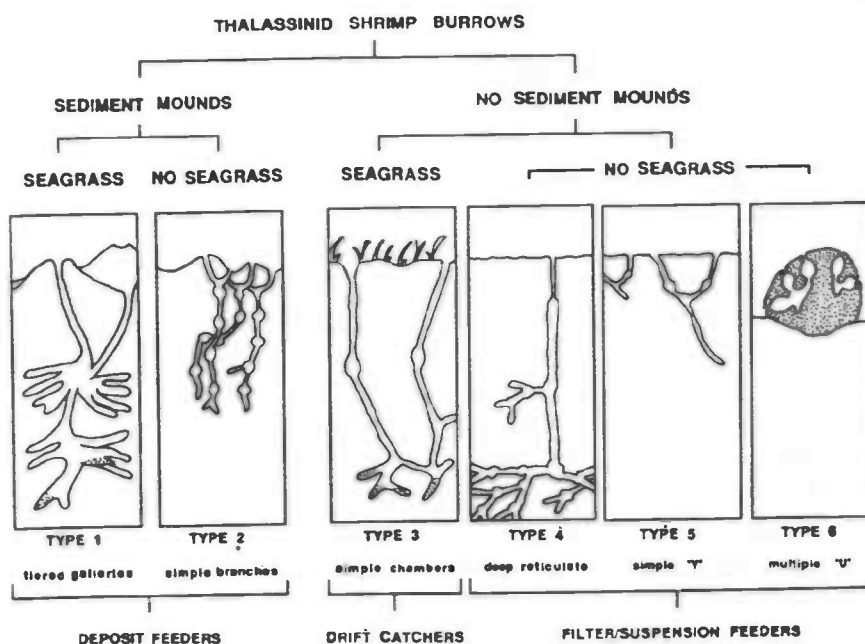


Figure 2: Griffis and Suchanek's classification model (22).

Griffis and Suchanek (22) made a classification into three trophic modes by using only two burrow characteristics: the presence of a mound at the surface and seagrass within the burrow. They classified all mound-building species into the deposit feeder category and the remaining species were classified into the group of drift catchers when seagrass was present in their burrows and when no seagrass was present they were classified into the suspension feeding group. They made a further classification of the deposit feeders and suspension feeders based on a whole set of characters. This model, that is based on assumptions regarding the importance of the characteristics for different feeding modes, rendered a total of six categories (fig 2; table 1).

**Table 1:** Classification of thalassinidean shrimp into 6 categories according to Griffis & Suchanek (1991).

| deposit feeders | | drift catchers | suspension feeders | | |
| ❶ | ❷ | ❸ | ❹ | ❺ | ❻ |
|---|---|---|---|---|---|
| C acanthochirus | C biformis | Axiopsis serratifrons | C guassetinga | C affinis | U ambomensis |
| Callichirus armatus | C bouvieri | Axius serratus | C jamaicense | U affinis | U operculata |
| Callichirus laurae | C californiensis | Callianidea laevicauda | C louisianensis | U africana | U synagelas |
| Glypturus motupore | C filholi | Corallianassa longiventris | Callichirus islagrande | U carinicauda | |
| Jaxea nocturna | C gigas | Neaxius sp. | Callichirus major | U deltaura | |
| | C guadracuta | | Glypturus jousseaumei | U macginitieorum | |
| | C japonica | | | U major | |
| | C kraussi | | | U pugettensis | |
| | C mirim | | | U pusilla | |
| | C pontica | | | U tipica | |
| | C rathbunae | | | | |
| | C subterranea | | | | |
| | C tyrrhena | | | | |
| | Calocaris macandreae | | | | |

About this model of Griffis and Suchanek, Nickell and Atkinson (35) argued that the data of a number of species did not fit into the categories. In their own words, 'burrow morphology of any species seems to be an amalgamation of several features from different categories'. They also argued that a distinction between simple Y and multiple U burrows should not have been made by Griffis and Suchanek because they are functionally similar in terms of trophic modes of inhabitants. Nickell and Atkinson probably based this on their own research which included three species, of which neither built a multiple U burrow. Since a multiple U burrow will have significantly more openings to the surface than a simple Y burrow, it could very well be possible that these burrow types differ in function regarding the trophic mode of the inhabitant. Nickell and Atkinson concluded that the model of Griffis and Suchanek was too simple to assign a trophic category to any species since each category was linked to merely one trophic mode while most burrows contain characteristics of more than one trophic mode.

The main goal of Nickell & Atkinson was to find a link between burrow morphology and the trophic mode of the inhabitant species. For 12 burrow characteristics, they determined for which trophic mode each characteristic was indicative. This rendered a rather complicated model, based on the burrows of three thalassinidean shrimps at the west coast of Scotland: *Callianassa subterranea*, *Jaxea nocturna* and *Upogebia stellata*. The characteristics they used were: presence of a mound, a tight layered lattice, the depth of the burrow, circular cross-section of the burrow tunnels, subcircular cross-section of the burrow wall, presence of chambers, presence of organic detritus, oblique tunnels, few or many openings, presence of a funnel shaped opening, a narrow exhalant shaft and a U/Y burrow type. In many cases, they thought of a burrow characteristic as indicative of more than one trophic mode (table 2). That makes it quite difficult to classify many species to one trophic category. In some cases a species will even end up in all three trophic modes. According to their own data, *Callianassa subterranea*, representative of the deposit feeders, could equally well be an omnivorous scavenger.

**Table 2:** Twelve features and the trophic modes they indicate, according to Nickell and Atkinson (1995)

| Feature | Trophic mode |
|---|---|
| Surface mound | deposit feeding |
| Tight layered lattice | deposit feeding |
| Deep burrow | deposit feeding |
| Subcircular tunnel cross-section | deposit feeding & omnivorous scavenging |
| Chambered burrows | deposit feeding & omnivorous scavenging |
| Organic detritus in burrow | omnivorous scavenging |
| Oblique tunnels | deposit feeding & omnivorous scavenging |
| Many burrow openings | deposit feeding & omnivorous scavenging |
| Funnel-shaped openings | deposit feeding & suspension feeding |
| Narrow exhalant shaft | deposit feeding & suspension feeding |
| U/Y burrow | deposit feeding & suspension feeding |
| Circular cross-section | deposit feeding & suspension feeding |

De Vaugelas (63) distinguished four trophic categories: deposit feeders, deposit-/resuspension feeders, primarily suspension feeders and seagrass-/algae harvesters. He renamed the latter to omnivorous scavengers. Regarding the deposit-/resuspension feeders, the burrow would be adapted to both trophic modes. Unlike Griffis and Suchanek and like Nickell and Atkinson, De Vaugelas took into account the fact that one burrow can contain characteristics of more than one trophic mode and the possibility that one species may use more than one feeding mechanism. But according to Nickell and Atkinson (35), some of the categories still did not adequately include all the morphological features seen within the burrow architecture of any particular species. They criticised the models of De Vaugelas and Griffis and Suchanek for being too specific and constructed their own model that is probably not specific enough.

## Goals

All of these models lead to groups of species that have similar burrows and should thus have a similar way of feeding (4, 56, 22, 35). In this thesis, burrow classification will be taken a step further by separating not only several groups from eachother, but by ultimately separating all species from eachother. A classification model was constructed that links the morphology of thalassinid burrows to the inhabitant species. Additionally, the model groups species together that have similar burrow systems and therefore possibly use similar feeding mechanisms. The model is based on a cluster analysis using 42 species of thalassinid shrimps in 9 genera.

## Methods

For as many species as possible, the following characteristics were gathered: the geographical location, the sediment type in which the burrow was built, the waterdepth and density of the shrimps, burrow type, maximum burrow depth, burrow volume, surface area, the permanence of a burrow system, the presence of chambers, seagrass, mounds and constricted openings, the number of surface openings, the diameter ratio of inhalant and exhalant openings (Øinhalant : Øexhalant), the numbers ratio of inhalant and exhalant openings (#inhalant : #exhalant) and the expelled sediment yield in grams per individual per day (table 3). The location, sediment type, waterdepth and animal density were eventually not included in the cluster analysis since these variables were not considered as burrow characteristics but as site characteristics. A relationship was found between the burrow volume and the surface area of the tunnels (power-regression: $R^2$=0.95; appendix Ia). This is not surprising since the volume of a tunnel can be calculated as "$\pi r^2 \times l$" (with $r$ being the radius of the tunnel and $l$ being the length of the tunnel) and the surface area as "$2\pi r \times l$". The relationship between the two variables can thus be characterized as: '*Volume = ½ x r x Surface Area*'. Because of this relationship, only the burrow volume was included in the analysis. Before a cluster analysis could be performed, it was necessary to calculate and determine mean values per species for each burrow characteristic.

'Tree clustering', also called 'joining', joins object (in this case: species) together in successively large clusters using some measure of similarity or distance. Using tree clustering, a model was constructed that has the appearance of a hierarchical tree. At each bifurcation, species can be divided into different groups based on a single burrow character.

### Advantages of tree clustering

Until now, models have been primarily based on assumptions regarding which characteristics are indicative of which trophic category. A classification of burrows using a cluster analysis will expectedly be less biased than the earlier models. Additionally, strong indication may be obtained concerning which features are important for such a classification and in what order. For instance, the characteristic 'number of openings' may be very important for separating species in the last stages of the classification tree, but it may not be of any importance at the first step of separation.

### The analysis

Tree clustering was performed with the program *Statistica 5.1*. The Euclidean distance, which is the geometric distance in a multidimensional space, was used as distance measure. The linkage rule used was 'Ward's method', which uses an ANOVA approach and attempts to minimize the sum of squares of two clusters. Missing values were substituted by means. The tree clustering algorithm constructs a hierarchical tree with the species scaled at one axis and the relative distance (Dlink/Dmax*100%) at the other (fig 3).

The cluster analysis was performed first using all species. The characters that were primarily responsible for division into clusters were determined by comparing the states of each character between and within the clusters. Characters that would explain more than 70% of the bifurcation were held responsible. All species were then again categorized according to these characteristics. Each category separately was consequently analyzed again using tree clustering and the characteristics that gave the closest fit to the different clusters were selected. According to these factors the species in that specific category were again categorized. This was repeated until all species were separated from eachother or until no further division could be made based on burrow characteristics. So in short: at each step the group of species concerned was divided into clusters using a cluster analysis, after that the feature that accounted the best for the division into clusters was determined and finally all species in the concerning group were again divided into clusters, this time not by means of a cluster analysis but 'by hand' according to the selected feature.

Division of all 42 species into two clusters, the first step, could be completely accounted for by the presence or absence of a mound. So consequently all species were categorized into two groups, based
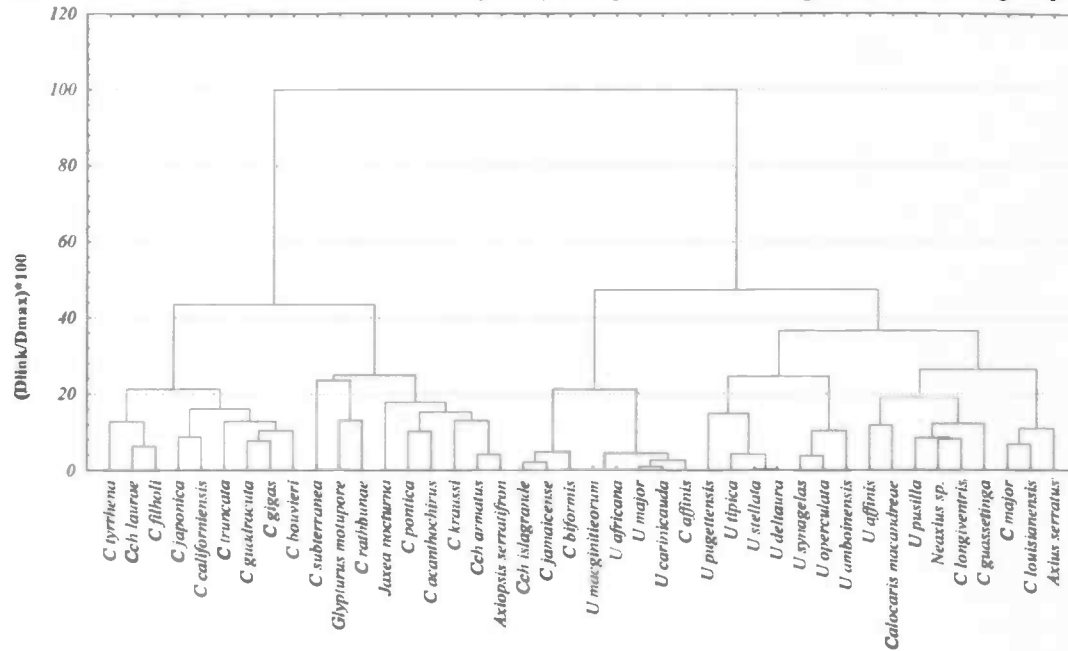


**Figure 3**: hierarchical tree including 42 species and 12 characteristics.

solely on this characteristic. Regarding the burrows with surface mounds, a further division could be accounted for by the waterdepth (79%), the number of openings (69%), the burrow volume (100%), the expelled sediment yield (89%) and the presence of chambers (92%). As far as the characteristics 'volume' and 'yield' are concerned, there were many missing data. Only for respectively 47% and 53% of the species, a value was known. So the division is best accounted for by the presence or absence of chambers. All burrows with mounds could thus be further categorized by this variable. The burrows with mounds and chambers were clustered into two groups and the maximum burrow depth accounted for this division with 100%. All burrows with a mound and without chambers were also clustered into two groups and the presence or absence of constricted openings accounted for this division for 100% although for 43% of the species, characteristics were missing.

The division of all burrows without a mound into two clusters could be accounted for by the waterdepth (82%), the number of openings (75%), the burrow type (77%) and the presence of seagrass (82%). Seagrass occurred significantly more in burrows in deeper water than in burrows in the intertidal (ANOVA: $p<0.05$) and the number of openings was related to burrow type with lattice burrows having significantly more openings (4.0 openings; ANOVA, $p<0.01$) than multiple U's (3.2), spiralling main tunnels (2.7), U/Y burrows (2.2) and single shafts (1.2). Since waterdepth had the closest fit to both clusters (82%), all burrows without a mound were categorized into those occurring mainly from 0 to 5 metres depth and those occurring deeper than 5 metres (according to appendix **Ib**).

All small clusters that were constructed in this way could be divided into single species by using all kinds of burrow features, including ones that were not taken into account in the cluster analysis. Basically all information that could be used to separate all species from eachother, was used.

## Similarity tree

While constructing the classification model, it became apparent that not all species that were included could be classified because critical data were missing. If these species were also to be included, these data should be filled in somehow. In order to achieve this, a tree including all 42 species was constructed that joined species with similar burrows. The missing data could consequently be derived from those species that were already included in the model and that were most similar to the species with missing data in terms of burrow morphology. The tree that was used to determine the first

**Table 3:** all 42 species and their burrow characteristics. All features under "Surface openings" and "Burrow" were included in the cluster analysis (inter=intertidal from 0-5 m, sub=subtidal deeper than 5 m, Locations: Mediterr=Mediterranean Sea, Papua NG=Papua New Guinea; References: 1)= in Griffis & Suchanek 1991, 3)= in de Vaugelas 1990a (62)).

| Species | Site characteristics | | | | Surface openings | | | | | Burrow | | | | | | | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Location | Substrate | Depth (m) | Density (n/m2) | O-ratio | N-ratio | N | Mound | Constr. | Type | Maxdepth (cm) | Volume (cm3) | Perm. | Yield (g/ind/day) | Grass | Chambers | |
| *Axiopsis serratifrons* | Caribbean | sand | 1 | 0,2 | | | 2,5 | 0 | | | | | | | 1 | 0 | 27 |
| *Axius serratus* | E USA | | 10 | 9,0 | | | 1,0 | 0 | | 3 | 250 | | | | | 0 | 39 |
| *Callianassa acanthochirus* | Caribbean | sand | inter/sub | | | | 2,0 | 1 | | 5 | 100 | | 0 | | | 1 | 31(2),44,46(2),52(1),55,56 |
| *Callianassa affinis* | W USA | gravel | inter | | | | 1,0 | 0 | | 1 | 51 | | 1 | | 1 | 0 | 29 |
| *Callianassa biformis* | E USA | mud | - | | | | 1,0 | 0 | | 3 | | | | | | 0 | 23(1) |
| *Callianassa bouvieri* | Red Sea | sand | inter | 323 | 2,2 | 1 | 2,0 | 1 | | 1 | 11 | 10 | | 34,7 | 0 | 0 | 15 |
| *Callianassa californiensis* | W USA | mudsand | inter | 120 | | | 2,1 | 1 | | 1 | 51 | 48 | | 39,8 | 1 | 0 | 21,29,41,54,57,60 |
| *Callianassa filholi* | N.Zealand | sand | 0,8 | 8,3 | | | 2,0 | 1 | | 4 | | | | | | 0 | 1,6 |
| *Callianassa gigas* | W USA | mudsand | inter | 300 | | | 2,4 | 1 | | 1 | 25 | 75 | | | 1 | 0 | 21,54 |
| *Callianassa guadracuta* | Caribbean | sand | 6 | | | | 2,0 | 1 | 0 | 1 | 150 | | | | | 0 | 55,56 |
| *Callianassa guasseitinga* | Brazil | - | inter | | | | 2,0 | 0 | | 3 | | | | | 0 | 0 | 47(2),48(2) |
| *Callianassa jamaicense* | Brazil | - | inter | | | | 1,0 | 0 | | 3 | | | | | 0 | 0 | 32,33,58,59 |
| *Callianassa japonica* | Japan | mudsand | inter | 591 | | | 2,0 | 1 | 1 | 1 | | 38,5 | 0 | | 0 | 0 | 9,18 |
| *Callianassa kraussi* | S Africa | sand | inter | | | | 1,0 | 0 | 0 | 3 | 200 | | | | 1 | 0 | 55,56 |
| *Callianassa longiventris* | Caribbean | sand | 7 | | | | 2,0 | 0 | | 1 | 150 | | | | 0 | 0 | 17(1),42(2) |
| *Callianassa louisianensis* | Caribbean | - | inter | | | | 1,5 | 0 | 0 | 3 | 250 | | | | 0 | 0 | 43,67 |
| *Callianassa major* | E USA | sand | inter | 0,3 | | | 1,0 | 0 | 0 | 3 | 212 | | | | | 0 | 12 |
| *Callianassa pontica* | Mediterr | sand | - | | | | 1,5 | 1 | | 3 | 79 | | 0 | | | 0 | 55 |
| *Callianassa rathbunae* | Caribbean | sand | 23 | 2,5 | 2,3 | 0,4 | 3,5 | 1 | 0 | 1 | 150 | | | 923 | 0 | 0 | 4,35,50,53,69 |
| *Callianassa subterranea* | North Sea,W-Scotland | mud | 31 | 27 | | 2,5 | 5,6 | 1 | 0 | 4 | 64 | 325 | 0 | 2,27 | | 0 | 70 |
| *Callianassa truncata* | Mediterr | sand | 9 | 120 | 1,8 | 2 | 3,0 | 1 | 0 | 1 | 50 | 60 | | 20,8 | 1 | 0 | 37 |
| *Callianassa tyrrhena* | Mediterr | sand | 0,4 | 16 | | 2,5 | 3,5 | 1 | | 4 | 25 | 50 | | 32,8 | 1 | 0 | 34 |
| *Calocaris macandreae* | W Scotland | mud | 23 | 0,2 | | | 4,8 | 0 | 0 | 2 | 215 | 477 | | 327 | 1 | | 61(1) |
| *Callichirus armatus* | Red Sea | mudsand | - | 1,5 | | | 1,5 | 1 | | 3 | | | | | 0 | | 42(2) |
| *Callichirus islagrande* | S USA | sand | inter | | | 1 | 2,0 | 0 | 0 | 4 | | | | 36,0 | 1 | 0 | 64(3),65 |
| *Callichirus laurae* | Red Sea | sand | 18 | 0,3 | | 0,6 | 2,0 | 0 | | 4 | 150 | | | 1376 | | 1 | 44 |
| *Glyp monapore* | Papua NG | mud | 15 | 0,3 | | | 5,5 | 1 | 0 | 5 | 91 | 2442 | 0 | | 0 | 1 | 35,40 |
| *Jaxea nocturna* | W.Scotland,Mediterr | mud | 11 | 0,1 | | | 3,0 | 1 | 0 | | 43 | | | | | | 16(1) |
| *Neaxius sp.* | India | - | | | | | 1,0 | 0 | | 1 | 50 | | | | | | 19(2),26(2),38 |
| *Upogebia affinis* | E USA | mud | inter | | | | 4,5 | 0 | | 1 | 60 | | | | 0 | | 24,25(2) |
| *Upogebia africana* | S Africa | mud | inter | | | | 2,0 | 0 | | 1 | 6 | | | | 0 | | 28(2) |
| *Upogebia amboinensis* | Australia | coral | sub | | | | 4,0 | 0 | | 2 | | | | | 0 | | 22 |
| *Upogebia carinicauda* | India | - | inter | | | 1 | 2,0 | 0 | | 1 | 28 | | | | | | 2 |
| *Upogebia deltaura* | W Scotland | mudsand | 20 | | | | 2,5 | 0 | | 1 | 60 | | | | 0 | 0 | 20(2),68 |
| *Upogebia macginitieorum* | W USA | sand | inter | | | | 2,0 | 0 | 0 | 1 | 30 | | | | 0 | 0 | 31,36(2) |
| *Upogebia major* | Japan | sand | inter | | | | 3,0 | 0 | | | 11 | 54 | | | 0 | 0 | 51 |
| *Upogebia operculata* | Caribbean | coral | 13 | 0,0 | | | 2,3 | 0 | | 1 | 89 | 1685 | | | 0 | 0 | 29,54,57,60,68 |
| *Upogebia pugettensis* | W USA | - | inter | 10 | | | 2,4 | 0 | 1 | 1 | 74 | 143 | 1 | | 1 | 0 | 11,12,13,14(2),37 |
| *Upogebia pusilla* | Mediterr | mudsand | inter/sub | 66 | | 1 | 2,5 | 0 | | 1 | 24 | 95 | | | | 0 | 2,35 |
| *Upogebia stellata* | W Scotland | mud | 14 | - | | | 2,0 | 0 | | 2 | 8 | 12 | | | | 1 | 51 |
| *Upogebia symagelas* | Caribbean | sponge | 26 | 9,3 | | | 2,3 | 0 | 1 | 2 | 28 | 70 | 1 | | 0 | 0 | 4,13,14(2) |
| *Upogebia typica* | Mediterr | sand | 14 | | | | | 0 | 0 | 1 | | | | | | 0 | |

characteristic to be used in the model (fig. **3**) resembled the model tree only slightly, possibly because while constructing the model, at every step all constructed clusters were isolated from eachother. This possibility was supported by a third tree. This time, like in the model, at every step all clusters were isolated from eachother and analyzed further until only small groups of species remained. Contrary to the model tree, no 'best fitting features' were determined and no manual classification took place. All dividing into clusters was done by means of a cluster analysis. This tree had a much greater resemblance to the model-tree. Apparently, the distribution of species within a cluster is influenced by the species from the other cluster(s). This effect is eliminated when the clusters are isolated from eachother. This third model, that will further be called the 'similarity tree', was used to assign species with missing values for critical characteristics to a place in the model.

An additional virtue of the similarity tree is that it allows for a check-up on whether the model-tree indeed groups species with similar burrows. The difference between the two trees is that in the model-tree, at each step the species were grouped according to the best fitting feature (as explained in the above section '*the analysis*'). Since those best-fitting feature practically never accounted for the division into clusters for 100%, at each step the model tree will deviate slightly further from the similarity tree. So does the model-tree still group species with similar burrows and thus similar feeding strategies?

To confirm that the model-tree really does, both the model-tree and the similarity tree were compared to eachother. The two main clusters in the model tree were isolated from eachother and in each tree, the presence or absence of chambers was traced in the cluster with mound-builders and in the other cluster, the tidal zone was traced (fig 5).

## Results

### Classification model

The classification model, constructed using tree clustering, is shown in figure 4. All species can be categorized into mound-building species and species with no mound surrounding the surface opening.

All mound building species can be divided into having chambers present in their burrows or not. Species that build mounds and have chambers present in their burrows can be divided into two different groups; those that build burrows up to a maximum depth of 80 centimetres and those that construct deeper burrows. The category with burrows shallower than 80 centimetres can be divided based on their burrow type. *C subterranea*, that fits into this category, constructs a lattice. The U/Y burrow systems can be divided based on the occurrence of seagrass in it. *C truncata* incorporates seagrass in the burrow, while *C bouvieri* does not. Those burrows that reach depths of up to more than 80 centimetres, can be divided in three categories according to the burrow type. *C kraussi*, fitting into this category of deep burrowers, constructs a single shaft burrow. Spiralling main tunnels (SMT) are constructed by three species; *Jaxea nocturna* constructs such a burrow in Scotland and the Adriatic (Europe), *C acanthochirus* at the southeast coast of the United States (Florida and the Virgin Islands) and *Glypturus motupore* constructs such burrows in New Guinea. The third category fitting in the group of deep burrowers with chambers and surface mounds, is made up by the constructors of U/Y burrows. *C rathbunae* keeps more than three openings to the surface while burrows of *C guadracuta* have less than three surface openings. Mound-builders that have no chambers other than turning chambers present in their burrows, can be divided into those with and those without constricted openings to the surface. Of the species with constricted openings in their burrow systems, a further division can be made based on the burrow type. *Callianassa pontica* constructs single shafts, *Callianassa filholi* a lattice burrow and the two U/Y burrowers can be divided based on the occurrence of seagrass in the burrows. While *C californiensis* incorporates seagrass in its burrow, *C japonica* does not. Those without constricted openings can be further divided into two categories based on their burrow type. U/Y burrows are built by *C gigas* and those that build lattice burrows, consisting of *Callichirus laurae* that lives in the subtidal and *C tyrrhena*, inhabiting the intertidal.

**Figure 4:** The classification model. The basis of the tree is outlined, all parts outside the border are called the 'derived portions'. Species that had missing data and were classified using the similarity tree are marked with a ' * '.

Species that do not build mounds can be divided in those that construct their burrows in the intertidal and shallow subtidal (to a waterdepth of 5 metres) and those that construct their burrows in the deeper subtidal (deeper than 5 metres). Species that live in deeper water can be divided into coral- and sponge dwellers and mud/sand dwellers. The sponge-dweller is *Upogebia synagels*. The coral dwellers can be further divided based on the number of surface openings, *U amboinensis* having more than three surface openings and *U operculata* with less than three openings. The mud/sand dwellers, finally, can be further divided into three categories, based on their burrow type. A single shaft is constructed by *Axius serratus*, a multiple U is built by *Calocaris macandreae* and constructors of lattice burrows can be divided based on the maximum burrow depth. *C longiventris* builds burrows that are up to more than 80 centimetres deep while burrows of *U pusilla* have a maximum depth between 40 and 80 centimetres. Of the shallowest burrows, with a maximum depth not exceeding 40 centimetres, in those of *U stellata* a funnel is present while *U deltaura* and *U tipica* differ from eachother regarding the distance between surface openings. In *U deltaura* burrows, openings are more than 10 centimetres apart while openings in *U tipica* burrows are 10 centimetres or less apart from eachother.

Of the non-mound-building species living from 0 to 5 metres depth, the constructors of U/Y burrows belong to a distinct category that can be further divided based on the maximum burrow depth. *U major* constructs relatively shallow burrows with a maximum depth less than 40 centimetres. *U pugettensis* constructs burrows that are deeper than 80 centimetres while the burrow with a maximum depth of up to 80 centimetres but deeper than 40 centimetres can be further divided based on the number of openings and the geographical location. *U affinis* is the one species that builds burrows with more than three openings to the surface. The remaining four species are *U africana*, living in South Africa, *U carinicauda* in India and *C affinis* and *U macginitieorum*, both living on the west coast of the United States. Regarding all burrow characteristics for which a value was known, the latter two species could not be separated from eachother.

Species that are non-mound-building, live in a waterdepth of 0 to 5 metres and construct 'Single shaft' burrows, can be divided into species that construct these burrows with only one opening to the surface and those that have more than one opening to the surface. Those with more than one opening to the surface, *C guassetinga*, *C louisianensis* and *Callichirus islagrande* could not be separated from eachother based on the known burrow information.

Of the species with a single shaft burrow, *C biformis* lives in mud while the two sand dwellers, *C major* and *C jamaicense* respectively occur at the east coast of the United States and in Brazil.


### Similarity tree

At first, *Callianassa affinis, C biformis, C filholi, C pontica, C tyrrhena, Glypturus motupore* and *Upogebia carinicauda* could not be included in the model because of missing characteristics. *Callianassa affinis* could not be included because it was not known whether or not this species builds surface mounds, *C biformis* because it was unclear in what tidal zone it burrows, *C filholi, C pontica* and *C tyrrhena* could not be classified because it was unknown if these species constrict their surface openings, for *Glypturus motupore* the burrow type was unknown and for *U carinicauda*, the maximum burrow depth was not known.

According to the similarity tree, *C affinis* is related to *U carinicauda, U africana* and *U macginitieorum*, all three mound-building species. Therefore, it was assumed that *C affinis* also builds surface mounds.

Furthermore, *C biformis* occurs in the same cluster as *C guassetinga, C louisianensis* and *Callichirus islagrande* and is therefore expected to inhabit the intertidal zone.

Since *C filholi* and *C pontica* were related the closest to *C californiensis* and *C japonica*, they were classified as having constricted openings. *C tyrrhena* was related the closest to *C gigas* and *Callichirus laurae*, both having constricted openings. Therefore it was assumed that *C tyrrhena* also constricts its openings.

*G motupore* was related closely to *Jaxea nocturna* and *Callianassa acanthochirus*, therefore a spiralling burrow type is most likely for this species.

Since *U carinicauda* was closest related to *U africana*, *U macginitieorum* and *C affinis*, maximum burrow depth will probably be between 40 and 80 centimetres deep.

Unfortunately, *Axiopsis serratifrons*, *Callichirus armatus* and *Neaxius sp.* could still not be included in the model because too many features were missing.
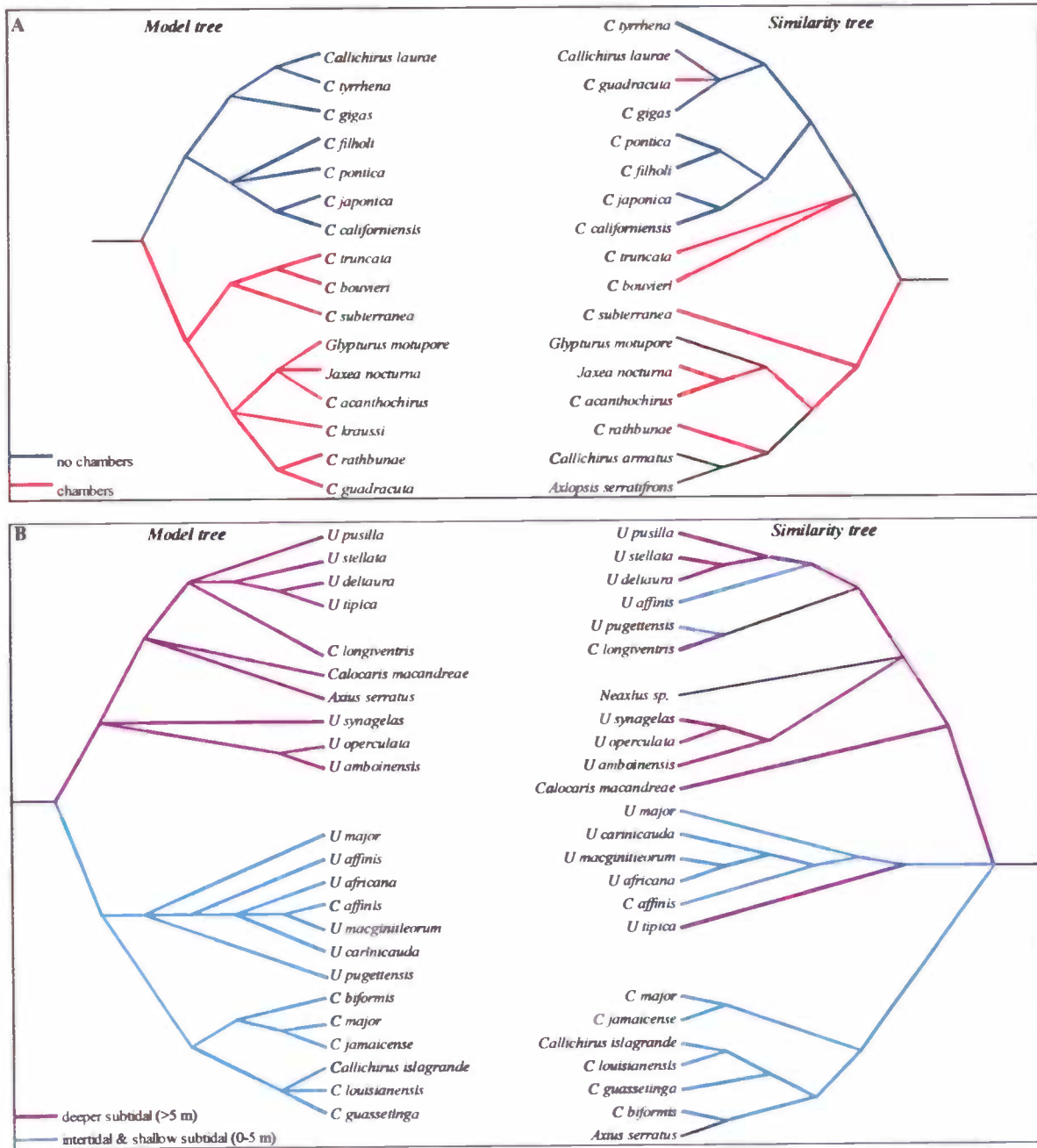


**Figure 5:** A comparison between the model tree (left) and the similarity tree (right). 4A: mound-builders, 4B: non mound-builders

When the model-tree is compared to the similarity tree, it is apparent that they correspond rather well. Differences between the two trees are few and of all species included in the model, approximately 80% occupies a similar position in both trees. That means that the model indeed groups species that have the most similar burrow systems and that should generally have the same feeding strategy.

*Earlier classification models*
The results of tree clustering were compared to the classification models of Griffis and Suchanek (22) and Nickell and Atkinson (35).

**Nickell & Atkinson**
To be able to make a comparison to this model, burrow characteristics of all species that were included in the cluster analysis had to be passed through that model in order to categorize them in the three trophic modes 'deposit feeders', 'suspension feeders' and 'omnivorous scavengers' (table 4). Four of their twelve burrow characteristics led to one single feeding strategy while the other eight

Table 4: Classification of thalassinidean shrimp into three trophic modes
according to the model of Nickell and Atkinson (1995)

| Deposit feeders | Filter feeders | Omnivorous scavengers |
|---|---|---|
| *Callianassa major* | *Callianassa affinis* | *Axiopsis serratifrons* |
| *Callianassa pontica* | *Upogebia africana* | *Neaxius sp.* |
| *Callichirus armatus* | *Upogebia carinicauda* | *Upogebia operculata* |
| *Callianassa acanthochirus* | *Upogebia deltaura* | |
| *Callianassa bouvieri* | *Upogebia macginitieorum* | |
| *Callianassa filholi* | *Upogebia major* | |
| *Callianassa guadracuta* | *Upogebia pugettensis* | |
| *Callianassa rathbunae* | *Upogebia stellata* | |
| *Calllanassa japonica* | *Upogebia tipica* | |
| *Callianassa subterranea* | | |
| *Callianassa truncata* | | |
| *Callianassa kraussi* | | |
| *Callianassa louisianensis* | | |

indicated two trophic modes. Because of that, it was rather exceptional to find species ending up in only one feeding strategy. Contrary to what one would expect and to the model of Griffis and Suchanek (22) and the model presented in this thesis, in the model of Nickell and Atkinson (35) more knowledge of an animal leads to more possibilities concerning the trophic category. The greater the certainty about burrow morphology, the greater the uncertainty regarding the trophic mode of the inhabiting animal. Species that ended up in the category 'omnivorous scavengers' only, or also in the mixed category 'omnivorous scavengers / deposit feeders' were considered to be omnivorous scavengers. Likewise, all species that could be classified only in the 'suspension- / deposit feeding' category were considered to be suspension feeders. All species that could be categorized into the group of 'deposit feeders' and in one or both of the other two categories that include deposit feeders were considered as such.
In table 4, all species that could be categorized into one trophic mode according to the model of Nickell and Atkinson (35), are shown in their trophic groups. *Calocaris macandreae, C acanthochirus, C californiensis, C truncata, Glypturus motupore* and *Jaxea nocturna* fitted in all three trophic groups and were no further taken into account regarding the comparison.
All ten 'filter feeders' turned out to be burrowers without surface mounds. Eleven out of thirteen 'deposit feeders' fitted into the cluster with mound-building species.
Ten out of thirteen deposit feeders are assigned to that trophic mode because of the presence of a surface mound while all filter feeders are assigned to that category based on their U/Y type of burrow. Of all species that were initially assigned to the suspension feeders only those remained that have a U/Y type of burrow and no mound or seagrass in their burrows. So, like in the model of Griffis and Suchanek (22), again all deposit feeders build a mound, all suspension- or filter feeders do not build mounds and all omnivorous scavengers (or drift catchers) do not build mounds and have seagrass incorporated in their burrows. In this model, the presence of a mound again plays an important role in the classification of species into trophic categories. This time, however, the presence of a mound was not selected to be the most important characteristic, it was one out of twelve equally important characteristics.

## Griffis & Suchanek

The two main clusters, mound-builders and non mound-builders, were compared to the three groups with similar feeding strategy according to Griffis and Suchanek (22). They assigned all mound-builders to the deposit feeding category and the remaining species to either 'filter feeders' or 'drift catchers', based on the presence of seagrass inside the burrows. So, not surprisingly, all mound-builders correspond with Griffis and Suchanek's deposit feeders, while all species that have no surface mounds surrounding their burrow openings are categorized into the other two trophic groups.

Looking at the six groups of species with similar burrow type, as presented by Griffis and Suchanek (table 1), there is a strong resemblance with the similarity tree (fig 6).
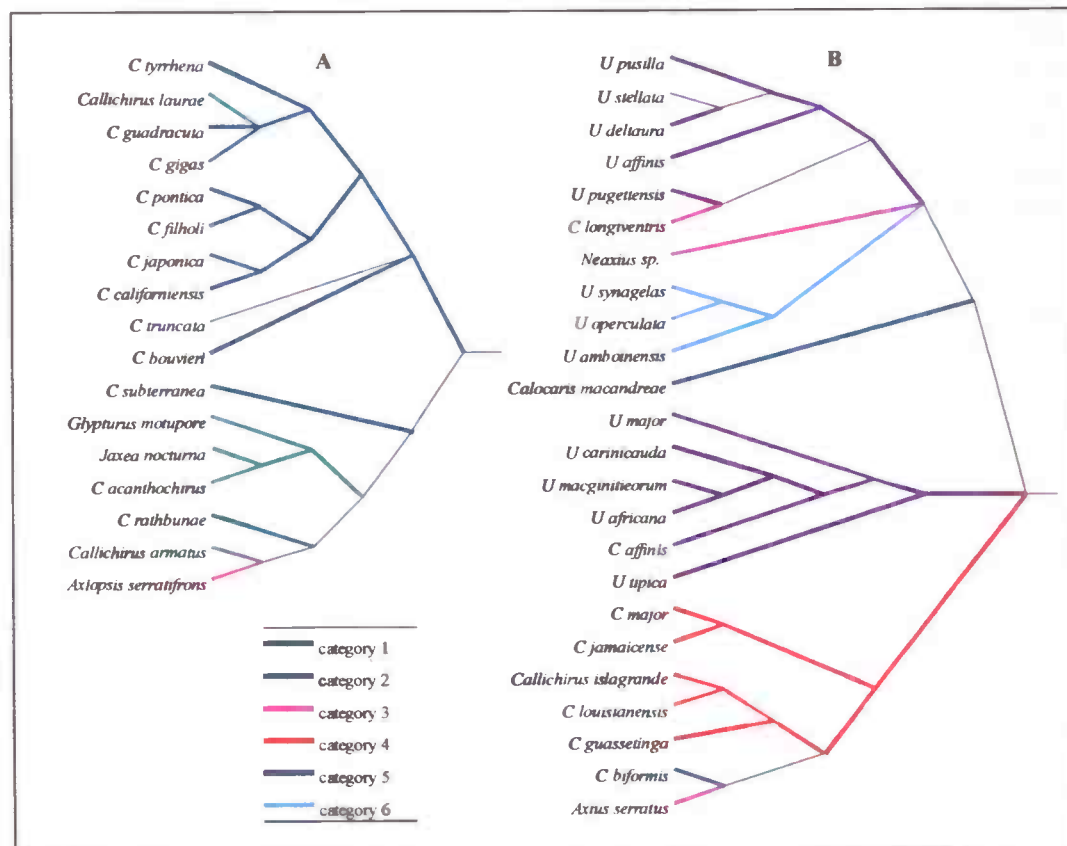


**Figure 6:** The similarity tree. 6A: mound-builders, 6B: non mound-builders. The branches are traced in 6 colours, corresponding with Griffis and Suchanek's categories (22)(fig. 2; table 1).

As mentioned before, practically all mound-builders are called deposit feeders by Griffis and Suchanek and are placed in the categories 1 and 2. Group 3, the drift catchers, are scattered all over the similarity tree but group 4, filter feeders, corresponds very well with the cluster that contains *C major, C jamaicense, Callichirus islagrande, C louisianensis, C guassetinga, C biformis* and *Axius serratus*. The differences are that according to Griffis and Suchanek, *Axius serratus* belongs to the drift catchers and *C biformis* to the deposit feeders. Species from group 5, also filter feeders, are distributed in the similarity tree in two clusters, the one containing *U pusilla, U stellata, U deltaura, U affinis, U pugettensis* and *C longiventris* and the other containing *U major, U carinicauda, U macginitieorum, U africana, C affinis* and *U tipica*. There was a 83% match between group 5 and the two clusters combined. Finally, group 6 corresponded exactly with the small cluster containing *U synagelas, U operculata* and *U amboinensis*.

The fact that there is a good correspondence between the classification of Griffis and Suchanek and the similarity tree, means that their categories already closely resembled groups of species with similar burrows as occurring in the field. However, this does not hold regarding the drift catchers. This group was scattered all over the similarity tree.

13

## Discussion

### Classification model

The basis of this model is expected not to change radically when more species are included. The features used in the first two levels of bifurcations fit the groups with similar burrows morphology very well, concerning the presence of a mound even for 100%, based on 42 species. Therefore, the base of the tree should be reliable. It is possible that the features used in the derived portions of the hierarchical tree will change when more species are added. But based on the dataset used in this thesis - in other words: based on practically all knowledge on thalassinidean burrow morphology to date - the features that were chosen at each step are the most suitable ones. These features were based in many cases on two to six species. When such a small group of species is joined by one or more 'new' species, the concerning feature may not have the best fit anymore. For instance, *Upogebia synagelas* was isolated from the other species living in the subtidal without surface mounds because of the fact that it burrows in a sponge. Although it was the only species burrowing in sponge that was included in the model, there are others that burrow in sponge as well (*Upogebia annae*: 51, *Axius inequalis*: 66). But of these sponge-burrowers not enough data were available to include them in the model. When more sponge burrowers are included, a new feature has to be found on which a division of these shrimps can be based. So the model may be altered in the derived portions and species may be added until the ultimate goal is reached: a model that includes all species of thalassinidean shrimps. Before that goal is reached, however, the model will prove a very useful determination scheme for burrows of all species that were included. It is important to realize that determination of a burrow will not lead to a single species with certainty, since there will always be the possibility that a species is dealt with that closely resembles the species of outcome but that is in fact a new species or a species that was not included in the model yet.

### Trophic modes

According to the cluster analysis, all 42 shrimps that were included can be classified into two main groups. Fairly all depositfeeders of Griffis and Suchanek (22) corresponded with the mound-building shrimps while all species with mound-less burrows corresponded with their filter feeders ánd their drift catchers. Assuming that indeed all mound-builders are deposit feeders and that all others are filter feeders and drift catchers, burrows of filter feeders and drift catchers are similar with regard to the burrows of deposit feeders. Therefore it is not likely that drift catching or gardening is a main feeding mechanism. It is more probable that this method is practised facultatively or as an additional feeding mechanism. All species that were assigned to this trophic mode by Griffis and Suchanek (22) ended up in the group of burrows without mounds. This will however be due to the fact that Griffis and Suchanek placed all mound-builders in the deposit feeding category, in spite of the presence of seagrass in some cases. There are mound-builders that also incorporate seagrass in their burow systems. Assuming that the organic material did not get there by accident but that it was introduced into the burrow actively, the presence of it suggests that it is important as a food source. Dworschak (13) observed that, after decomposition, introduced seagrass was incorporated in the burrow wall by the resident shrimp. Therefore, this gardening behaviour will not be restricted to filter feeders, it can also be practised by certain deposit feeders, like *Callianassa truncata* (70) and *Callianassa californiensis* (54, 29, 60, 41, 57, 21), whose burrows contained seagrass.

14

# References

1. Allanson, B.R., D. Skinner & J. Imberger, 1992: "Flow in prawn burrows." *Estuarine, Coastal and Shelf Science, 35: 253-266.*

2. Astall, C.M., A.C. Taylor & R.J.A. Atkinson, 1997: "Behavioural and physiological implications of a burrow-dwelling lifestyle for two species of Upogebiid mud-shrimp (Crustacea: Thalassinidea)." *Estuarine, Coastal and Shelf Science, 44: 155-168.*

3. Atkinson, R.J.A. & C.J. Chapman, 1984: "Resin casting: a technique for investigating burrows in sublittoral sediments." *Progr. Underwat. Sci., 10: 109-115.*

4. Atkinson, R.J.A. & R.D.M. Nash, 1990: "Some preliminary observations on the burrows of *Callianassa subterranea* (Montagu) (Decapoda: Thalassinidea) from the west coast of Scotland." *Journal of Natural History, 24: 403-413.*

5. Atkinson, R.J.A., C. Froglia, E. Arneri & B. Antolini, 1998: "Observations on the burrows and burrowing behaviour of *Brachynotus gemmellari* and on the burrows of several other species occurring on *Squilla* grounds off Ancona, Central Adriatic." *Scientia Marina, 62(1-2): 91-100.*

6. Berkenbusch, K. & A.A. Rowden, 1999: "Factors influencing sediment turnover by the burrowing ghost shrimp *Callianassa filholi* (Decapoda: Thalassinidea)." *Journal of Experimental Marine Biology and Ecology, 238: 283-292.*

7. Biffar, T.A., 1971: "The genus *Callianassa* (Crustacea, Decapoda, Thalassinidea) in South Florida, with keys to the western Atlantic species." *Bulletin of Marine Science, 21(3): 637-715.*

8. Braithwaite, C.J.R. & M.R. Talbot, 1972: "Crustacean burrows in the Seychelles, Indian Ocean." *Palaeogeography, Palaeoclimatology, Palaeoecology, 11: 265-285.*

9. Branch, G.M. & A. Pringle, 1987: "The impact of the sand prawn *Callianassa kraussi* Stebbing on sediment turnover and on bacteria, meiofauna, and benthic microflora." *Journal of Experimental Marine Biology and Ecology, 107: 219-235.*

10. Devine, C.E., 1966: "Ecology of *Callianassa filholi* Milne-Edwards 1878 (Crustacea, Thalassinidea)." *Trans. R. Soc. N. Z., Zool., 8: 93-110.*

11. Dworschak, P.C., 1981: "The pumping rates of the burrowing shrimp *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea)." *Journal of Experimental Marine Biology and Ecology, 52: 25-35.*

12. Dworschak, P.C., 1983: "The biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidea) - I. The burrows." *Marine Ecology, 4(1): 19-43.*

13. Dworschak, P.C., 1987a: "Feeding behaviour of *Upogebia pusilla* and *Callianassa tyrrhena* (Crustacea, Decapoda, Thalassinidea)." *Inv. Pesq., 51(1): 421-429.*

14. Dworschak, P.C., 1987b: "Burrows of Mediterranean decapoda." *Investigación Pesquera, 51(1): 264.*

15. Dworschak, P.C. & P. Pervesler, 1988: "Burrows of *Callianassa bouvieri* Nobili 1904 from Safaga (Egypt, Red Sea) with some remarks on the biology of the species." *Senckenbergiana Maritima, 20(1-2): 1-7.*

16. Farrow, G.E., 1971: " Back-reef and lagoonal environments of Aldabra Atoll distinguished by their crustacean burrows." *Symp. Zool. Soc., London, 28: 455-500.*

17. Felder , D.L., J.L. Staton, & R.B. Griffis, 1990: "Relationships of burrow morphology to population structure in the estuarine ghost shrimp *Lepidothalmus louisianensis* (Decapoda, Thalassinidea)." *Am. Zool., 30(4): 137A.*

18. Forbes, A.T., 1973: "An unusual abbreviated larval life in the estuarine burrowing prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassinidea)." *Marine Biology, 22: 361-365.*

19. Frey, R.W. & J.D. Howard, 1975: "Endobenthic adaptations of juvenile thalassinidean shrimp." *Bull. Geol. Soc. Den., 24: 283-297.*

20. Griffis, R.B., 1988: "Behavioral interactions between burrowing shrimp: effects on distribution of sympatric thalassinids." *Am. Zool., 28(4): 179A.*

21. Griffis, R.B. & F.L. Chavez, 1988: "Effects of sediment type on burrows of *Callianassa californiensis* Dana and *C. gigas* Dana." *Journal of Experimental Marine Biology and Ecology, 117: 239-253.*

22. Griffis, R.B. & T.H. Suchanek, 1991: "A model of burrow architecture and trophic modes in thalassinidean shrimp (Decapoda: Thalassinidea)." *Marine Ecology Progress Series, 79: 171-183.*

23. Hertweck, G., 1972: "Georgia coastal region, Sapelo Island, U.S.A.: Sedimentology and biology. V. Distribution and environmental significance of Lebensspuren and *in-situ* skeletal remains." *Senckenbergiana maritima, 4: 125-167.*

24. Hill, B.J. & B.R. Allanson, 1971: "Temperature tolerance of the estuarine prawn *Upogebia africana* (Anomura, Crustacea)." *Marine Biology, 11: 337-343.*

25. Hill, B.J., 1971: "Osmoregulation by an estuarine and a marine species of *Upogebia* (Anomura, Crustacea)." *Zool. Afr., 6(2): 229-236.*

26. Howard, J.D. & R.W. Frey, 1975: "Estuaries of the Georgia Coast, U.S.A.: Sedimentology and biology II. Regional animal-sediment characteristics of Georgia estuaries." *Senckenbergiana maritima, 7: 33-103.*

27. Kensley, B., 1980: "Notes on *Axiopsis* (Axiopsis) *serratifrons* (A. Milne Edwards) (Crustacea, Decapoda, Thalassinidea)." *Proc. Biol. Soc. Wash., 93(4): 1253-1263.*

28. Kleemann, K.K., 1984: "Lebensspuren von *Upogebia operculata* (Crustacea, Decapoda) in karibischen Steinkorallen (Madreporaria, Anthozoa)." *Beitr. Palaeontol. Österr., 11: 35-57.*

29. MacGinitie, G.E. & N. MacGinitie, 1968: "Natural History of marine animals" *2nd ed., McGraw-Hill, New York, 473 pp.*

30. Manning, R.B., 1975: "Two methods for collecting decapods in shallow water." *Crustaceana, 29: 317-319.*

31. Manning, R.B., 1987: "Notes on Western Atlantic Callianassidae (Crustacea; Decapoda; Thalassinidea)." *Proc. Biol. Soc. Wash., 100(2): 386-401.*

32. Mukai, H. & I. Koike, 1984a: "Behavior and respiration of the burrowing shrimps *Upogebia major* (De Haan) and *Callianassa japonica* (De Haan)." *Journal of Crustacean Biology, 4(2): 191-200.*

33. Mukai, H. & I. Koike, 1984b: "Pumping rates of the mud shrimp *Callianassa japonica*." *Journal of the Oceanographical Society of Japan, 40: 243-246.*

34. Nash, R.D.M., C.J. Chapman, R.J.A. Atkinson & P.J. Morgan, 1984: "Observations on the burrows and burrowing behaviour of *Calocaris macandreae* (Crustacea: Decapoda: Thalassinoidea)." *Journal of Zoology London, 202: 425-439.*

35. Nickell, L.A. & R.J.A. Atkinson, 1995: "Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology." *Marine Ecology Progress Series, 128: 181-197.*

36. Ohshima, K., 1967: "Burrows of Japanese Thalassinidea." *Chikyu Kagaku, 21(1): 11-18.*

37. Ott, J.A., B. Fuchs, R. Fuchs & A. Malasek, 1976: "Observations on the biology of *Callianassa stebbingi* Borrodaille and *Upogebia litoralis* Risso and their effect upon the sediment." *Senckenbergiana Maritima, 8(1-3): 61-79.*

38. Pearse, A.S., 1945: "Notes and comment - Ecology of *Upogebia affinis* (Say)" *Ecology, 26(3): 303-305.*

39. Pemberton, G.S., M.J. Risk & D.E. Buckley, 1976: "Supershrimp: deep bioturbation in the Strait of Canso, Nova Scotia." *Science, 192: 790-791.*

40. Pervesler, P. & P.C. Dworschak, 1985: "Burrows of *Jaxea nocturna* Nardo in the Gulf of Trieste." *Senckenbergiana Maritima, 17(1-3): 33-53.*

41. Peterson, C.H., 1977: "Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons." *Marine Biology, 43: 343-359.*

42. Phillips, P.J., 1971: "Observations on the biology of mud-shrimps of the genus Callianassa (Anomura: Thalassinidea) in Mississippi Sound." *Gulf Res. Reps., 3: 165-196.*

43. Pohl, M.E., 1946: "Ecological observations on *Callianassa major* Say at Beaufort, North Carolina." *Ecology, 27(1): 71-80.*

44. Poore, G.C.B. & T.H. Suchanek, 1988: "*Glypturus motupore*, a new callianassid shrimp (Crustacea; Decapoda) from Papua New Guinea with notes on its ecology." *Rec. Aut. Mus., 40: 197-204.*

45. Rice, A.L. & C.J. Chapman, 1971: "Observations on the burrows and burrowing behavior of the mud-dwelling crustaceans, *Nephrops norvegicus* and *Goneplax rhomboides*." *Mar. Biol., 10: 330-342.*

46. Roberts, R.R., T.H. Suchanek & W.J. Wiseman, 1982: "Lagoon sediment transport: the significant effect of *Callianassa* bioturbation." *Proc. 4th Int. Coral Reefs Symp., Manila.*

47. Rodrigues, S. de A., 1966: "Estudos sôbre *Callianassa*. Sistemática, biologia e anatomia." *Dissertation, University of São Paulo, Brazil, 168 pp.*

48. Rodrigues, S. de A., 1971: "Mud shrimps of the genus *Callianassa* Leach from the Brazilian coast (Crustacea, Decapoda)." *Arq. Zool., São paulo, 20(3): 191-223.*

49. Rowden, A.A. & M.B. Jones, 1995: "The burrow structure of the mud shrimp *Callianassa subterranea* (Decapoda: Thalassinidea) from the North Sea." *Journal of Natural History, 29: 1155-1165.*

50. Rowden, A.A., M.B. Jones & A.W. Morris, 1998: "The role of *Callianassa subterranea* (Montagu) (Thalassinidea) in sediment resuspension in the North Sea." *Cont. Shelf. Res., 18: 1365-1380.*

51. Scott, P.J.B., H.M. Reiswig & B.M. Marcotte, 1987: "Ecology, functional morphology, behaviour, and feeding in coral- and sponge-boring species of *Upogebia* (Crustacea: Decapoda: Thalassinidea)." *Canadian Journal of Zoology, 66: 483-495.*

52. Shinn, E.A., 1968: "Burrowing in recent lime sediments of Florida and the Bahamas." *J. Paleontol., 42(4): 879-894.*

53. Stamhuis, E.J., C.E. Schreurs & J.J. Videler, 1997: "Burrow architecture and turbative activity of the thalassinid shrimp *Callianassa subterranea* from the central North Sea." *Marine Ecology Progress Series, 151: 155-163.*

54. Stevens, B.A., 1929: "Ecological observations on Callianassidae of Puget Sound." *Ecology, 10(4): 399-405.*

55. Suchanek, T.H., 1983: "Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation." *Journal of Marine Research, 41: 281-298.*

56. Suchanek, T., 1985: "Thalassinid shrimp burrows: ecological significance of species-specific architecture." *Proceedings of the Fifth International Coral Reef Congress, Tahiti, vol. 5.*

57. Swinbanks, D.D. & J.L. Luternauer, 1987: "Burrow distribution of thalassinidean shrimp on a Fraser delta tidal flat, British Columbia." *J. Paleont., 61(2): 315-332.*

58. Tamaki, A., 1988: "Effects of the bioturbating activity of the ghost shrimp *Callianassa japonica* Ortmann on migration of a mobile polychaete." *Journal of Experimental Marine Biology and Ecology, 120: 81-95.*

59. Tamaki, A., B. Ingole, K. Ikebe, K. Muramatsu, M. Taka & M. Tanaka, 1997: "Life history of the ghost shrimp, *Callianassa japonica* Ortmann (Decapoda: Thalassinidea), on an intertidal sandflat in western Kyushu, Japan." *Journal of Experimental Marine Biology and Ecology, 210: 223-250.*

60. Thompson, R.G. & A.W. Pritchard, 1969: "Respiratory adaptations of two burrowing crustaceans, *Callianassa californiensis* and *Upogebia pugettensis* (Decapoda, Thalassinidea)." *Biol. Bull., 136: 274-287.*

61. Vaugelas, J. de, B. Delesalle & C. Monier, 1986: "Aspects of the biology of *Callichirus armatus*, A. Milne Edward 1870 (Crustacea, Thalassinidea) from French Polynesia." *Crustaceana, 50: 204-216.*

62. Vaugelas, J. de, 1990a: "Sediment reworking by Callianassid mud-shrimp in tropical lagoons: A review with perspectives." *Proc. 5th Int. Coral Reef Congress, Tahiti, vol. 6.*

63. Vaugelas, J.V. de, 1990b: "Ecologie des callianasses (Crustacea, Decapoda, Thalassinidea) et milieu récifal Indo-Pacifique. Conséquences du remaniement sédimentaire sur la distribution des matieres humiques, de métaux trace et des radionucléides." *Mémoire présenté a l'Université de Nice, p 1-269.*

64. Vaugelas, J. de & M. de Saint Laurent, 1984: "Premières données sur l'écologie de *Callichirus laurae* (de Saint Laurent), sp. nov., (*Crustacea, Thalassinidea*): son action bioturbatrice sur les formations sédimentaires du Golfe d'Aqaba (Mer Rouge)." *C.r. Acad. Sci., Paris t.298, ser. III, 6: 147-152.*

65. Vaugelas, J. de & R. Buscail, 1990: "Organic matter distribution in burrows of the thalassinid crustacean *Callichirus laurae*, Gulf of Aqaba (Red Sea)." *Hydrobiologia, 207: 269-277.*

66. Westinga, E. & P.C. Hoetjes, 1981: "The intrasponge fauna of *Spheciospongia vesparia* (Porifera, Demospongiae) at Curaçao and Bonaire." *Mar. Biol., 62: 139-150.*

67. Weimer, R.J. & J.H. Hoyt, 1964: "Burrows of *Callianassa major* Say, geologic indicators of littoral and shallow neritic environments." *Journal of Paleontology, 38(4): 761-767.*

68. Williams, A.B., 1986: "Mud shrimps, *Upogebia*, from the eastern Pacific (Thalassinoidea: Upogebiidae)." *Society of Natural History San Diego, Memoir 14.*

69. Witbaard, R. & G.C.A. Duineveld, 1989: "Some aspects of the biology and ecology of the burrowing shrimp *Callianassa subterranea* (Montagu) (Thalassinidea) from the southern North Sea." *Sarsia, 74: 209-219.*

70. Ziebis, W., S. Forster, M. Huettel & B.B. Jørgensen, 1996: "Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea bed." *Nature, 382: 619-622.*

# Appendix
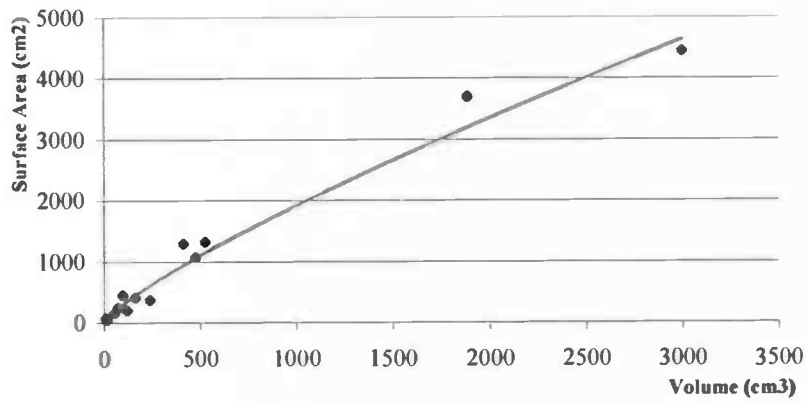


**Appendix Ia:** The relationship between burrow volume and surface area of the tunnels (power regression, R2=0.95)
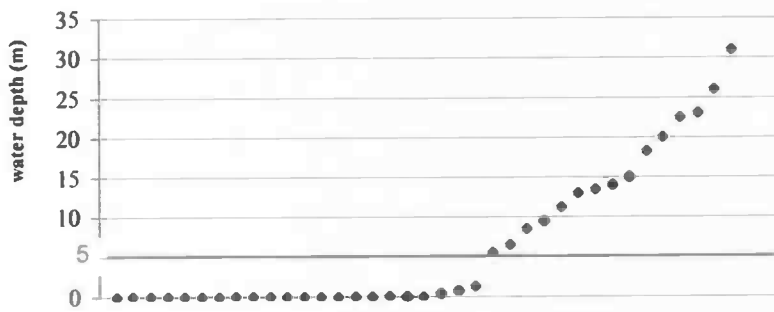


**Appendix Ib:** Waterdepths for all species a value was known for. Each marker represents one species