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Intraspecific burrow plasticity of an intertidal population of *Callianassa filholi* (Crustacea: Decapoda: Thalassinidea) in relation to environmental conditions

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Abstract Burrow morphology and intraspecific burrow plasticity in relation to environmental conditions were examined for an intertidal population of *Callianassa filholi* Milne-Edwards, 1878 in south-eastern New Zealand. Multivariate analysis of burrow features revealed no significant differences in burrow morphology between seasons. However, dissimilarities between burrows from different seasons could be identified and included differences in lateral extent, total length, and volume of burrows. These size parameters each showed low values in winter, coinciding with low seawater temperature and high organic content of the sediment. There was no significant relationship between any of the three size parameters and sediment grain size or shore height of the burrow, but lateral extent and total length of the burrow were significantly related to organic content of the sediment, decreasing with increasing organic content. Furthermore, there was a significant positive relationship between seawater temperature and total length of the burrow. Data from the present study imply that intraspecific variation in burrow morphology for callianassids is dependent on environmental variables, which has consequences for the construction of useful burrow models.

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INTRODUCTION

Thalassinidean shrimps construct burrows in intertidal and subtidal soft sediments (Posey 1985; Witbaard & Duineveld 1989). Their burrows are considered to be amongst the deepest (>50 cm) and most complex decapod burrows (Dworschak 1983; Atkinson & Taylor 1988), and are used for shelter, reproduction, and feeding; most thalassinideans live exclusively within the burrow, except for a brief pelagic stage (Griffis & Suchanek 1991). The morphology of thalassinidean burrows has intrigued geologists, paleoecologists, and marine ecologists for a number of years (MacGinitie 1934; Weimer & Hoyt 1964; Frey & Howard 1975), but depth and complexity of the burrows have impeded studies on burrow architecture until the relative recent advent of epoxy and polyester resins (Shinn 1968). Use of resin has enabled detailed casts of entire burrow systems to be obtained (Atkinson & Chapman 1984) and has allowed investigations into the burrow morphology for a variety of thalassinidean species (Tudhope & Scoffin 1984; Vaugelas 1984; Dworschak & Pervesler 1988). Studies document high levels of variation in burrow architecture (see review Dworschak 1983), and it has been suggested that burrow types reflect species-specific differences in feeding mode (Suchanek 1985; Vaugelas 1990; Griffis & Suchanek 1991). However, burrow classification models based on trophic modes fail to account for intraspecific variation in burrow morphology, even though improvements to such models have been proposed recently (Nickell & Atkinson 1995). Intraspecific burrow plasticity has been linked to biological factors (e.g., population density (Nash et al. 1984); space-resource competition with associated macro-infauna (Peterson 1977)), and environmental conditions (e.g., sediment type (Griffis & Chavez 1988); organic content (Rowden & Jones 1995)).

The difficulty in casting burrows in sufficient numbers has prevented comprehensive studies of intraspecific burrow plasticity in general, and, therefore, the influence of biological and environmental variables has not yet been adequately established. The present study aims to address this shortfall by assessing burrow plasticity of the ghost shrimp *Callianassa filholi* Milne-Edwards, 1878 in relation to time and associated environmental factors. *C. filholi* is endemic to New Zealand and is one of the few Southern Hemisphere temperate species of callianassid shrimp to have received any biological investigation (Berkenbusch & Rowden 1998, 1999; Berkenbusch et al. 2000). To date, information on the burrow morphology has been limited to general observations (Devine 1966). This lack of information provided the impetus to determine the general burrow morphology, and to assess seasonal burrow plasticity, of an intertidal *C. filholi* population.

MATERIALS AND METHODS

Burrow morphology of an intertidal population of *Callianassa filholi* in south-eastern New Zealand (170°42′ E, 45°30′S) was investigated *in situ* on an uniformly sloping sandflat with a tidal range of 1.4–2.2 m (Fig. 1). Burrows were cast monthly from May 1995 to August 1996, and seasonally from August 1997 to July 1998, using epoxy resin (Ciba Speciality Chemicals NZ Ltd, Araldite GY 9513, LC 191, and Hardener HY 2992, 2996; density range = 1.05–1.25 g cm^{-3}). On each casting occasion, 10 burrows were haphazardly selected on the sandflat and resin was poured into plastic sleeves (bottomless plastic containers, diameter 10 cm and 20 cm) placed around burrow openings. The horizontal distance of each burrow cast in relation to the shore was established as a proxy measure of tidal height. In addition, on each casting occasion sediment cores were taken (diameter 3 cm, 10 cm depth) for granulometry and organic content analysis. Seawater temperature was measured at the Portobello Marine Laboratory, in close proximity (11 km) to the study site.

Resin was left in the burrows to cure for 24 h before the casts were excavated by hand. After excavation, casts (the surfaces of which were initially sticky) were allowed to further harden in air, before being weighed (±0.01 g) and measured (tape measure and digital sliding handcalipers, ±0.01 mm). Burrow measurements taken were: (1) maximum depth; (2) depth of the junction between the horizontal burrow system and shafts to the surface; (3) number, mean length, and diameter of shafts to the surface (inhalant and exhalant); (4) length, width, and height of exhalant nodule(s); (5) mean length and diameter of tunnels; (6) mean length and diameter of shafts; (7) number, length, width, and height of turning chambers; (8) number of turning chamber insections; (9) number of terminal turning chambers; (10) number of dead ends; (11) total length of tunnels and turning chambers (lateral extent); (12) total length of the burrow system (lateral extent and total length of vertical shafts); and (13) number, length, width, and height of sumps. For the diameter of each separate shaft and tunnel a mean value was calculated from three equidistant measurements. For some burrow features, such as exhalant nodules, turning chambers and sumps, maximum measurements (length, width, and height) were taken.

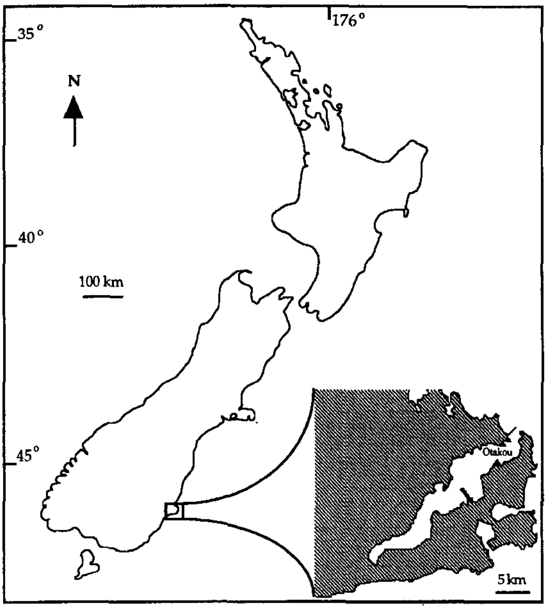

Fig. 1 Intertidal study site at Otakou, Otago Harbour, south-eastern New Zealand.

Burrow volume was calculated using the weight of the burrow and the specific density of the resin ascertained for each sampling occasion. Some of the casts were partially covered in a thin layer of sand (presumably where the burrow wall was not lined with mucus), and to adjust the calculation of the respective burrow volume for this feature, calibration cubes covered in sand were cast. The ascertained correction factor, together with thickness of the sand layer and percentage cover of the casts, were used to derive individually-adjusted volume measures (correction between 9 and 44% of initial volume).

Entombed shrimp were visible in six burrow casts, one of which showed two shrimp in different parts of the burrow, but because of the opaque nature of the casts, morphological measurements of entombed shrimp were precluded. Because of insufficient penetration, burrow casts were frequently incomplete (including the burrow shared by two shrimp), and not all dimensions could be measured. However, 35 casts were deemed "complete" enough (indicated by the condition/appearance of the ends of shafts and tunnels) to be used to describe the general burrow characteristics of *C. filholi*, and for subsequent statistical analysis of burrow plasticity.

Sediment grain size was ascertained by sieving at 1 phi-intervals from 1 mm to 63 µm (Buchanan 1984), and sediment sorting was determined using the program Rapid Sediment Analysis v. 7.1 (developed by the University of Waikato, New Zealand). Organic content was determined by loss of weight on ignition (4 h at 500°C).

Data analysis

Depending on the sampling occasion, casts were classed into spring ($n = 6$), summer ($n = 9$), autumn ($n = 7$), and winter ($n = 13$). Casts from each season reflected a range of shrimp sizes as indicated by the diameter of shafts/tunnels, which are known to be related to the size of the constructing individual (Dworschak & Pervesler 1988; Rowden & Jones 1995). Differences in burrow morphology were assessed by multivariate analysis, using the software package PRIMER (see Clarke & Warwick 1994). Designed to analyse differences in community structure, PRIMER accounts for the compsition of species amongst samples; in the present study it was applied to the combination of morphological features ascertained for each burrow. A triangular similarity matrix was computed based on the Bray-Curtis coefficient on $\sqrt{}$-transformed data (Bray & Curtis 1957). Data were transformed to account for less common burrow features in the similarity matrix (Clarke & Warwick 1994). Subsequent hierarchical, agglomerative cluster analysis involved group-average linking and was displayed in a dendrogram (Gray et al. 1988). Seasonal differences in burrow morphology were assessed by using 1-way ANOSIM permutation tests (Clarke & Green 1988). Burrow features that contributed to dissimilarities in burrow morphology were ascertained by the similarities percentages procedure SIMPER (Clarke 1993). The relationship between each burrow feature that contributed to seasonal differences and environmental variables (sediment grain size, organic content, seawater temperature, and shore height of the burrow) was determined by linear least squares regressions (Zar 1984).

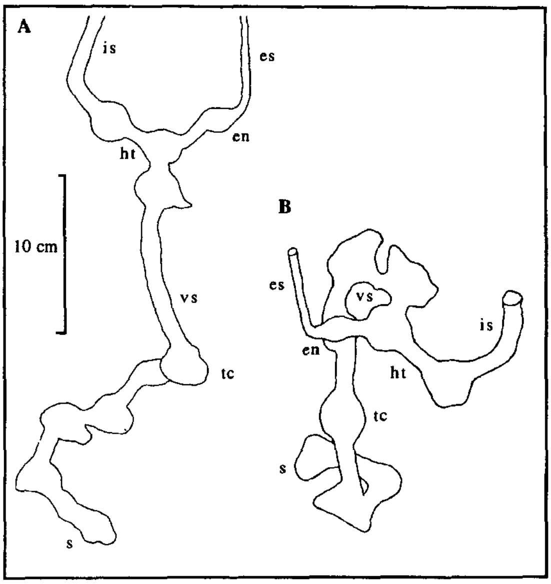

Fig. 2 Drawing of a typical burrow constructed by *Callianassa filholi*: **A**, lateral view; and **B**, plan view. (Key to burrow features: is = inhalant shaft; es = exhalant shaft; en = exhalant nodule; vs = vertical shaft; ht = horizontal tunnel; tc = turning chamber; and s = sump.)

RESULTS

General burrow morphology

Resin casts of 35 complete burrows showed that *C. filholi* constructs complex burrows with a similar general morphology (refer to Fig. 2 during following description) (see Appendix 1 for burrow measurements). Burrows were connected to the sediment surface by a number of vertical shafts, which were functionally either inhalant (1–2) or exhalant (1–3). Exhalant shafts (es) were generally longer than inhalant shafts (is) (mean/standard deviation (SD) = 8.3/2.4 and 6.4/2.9 cm, respectively), and half the diameter of the inhalant ones (0.5/0.2 and 1/0.3 cm, respectively). Furthermore, exhalant shafts were each characterised by an exhalant nodule (en) at the base, the form of which was consistent throughout all burrow casts. The main burrow system generally comprised a single route of short horizontal tunnels (ht) and vertical shafts (vs). Turning chambers (tc),

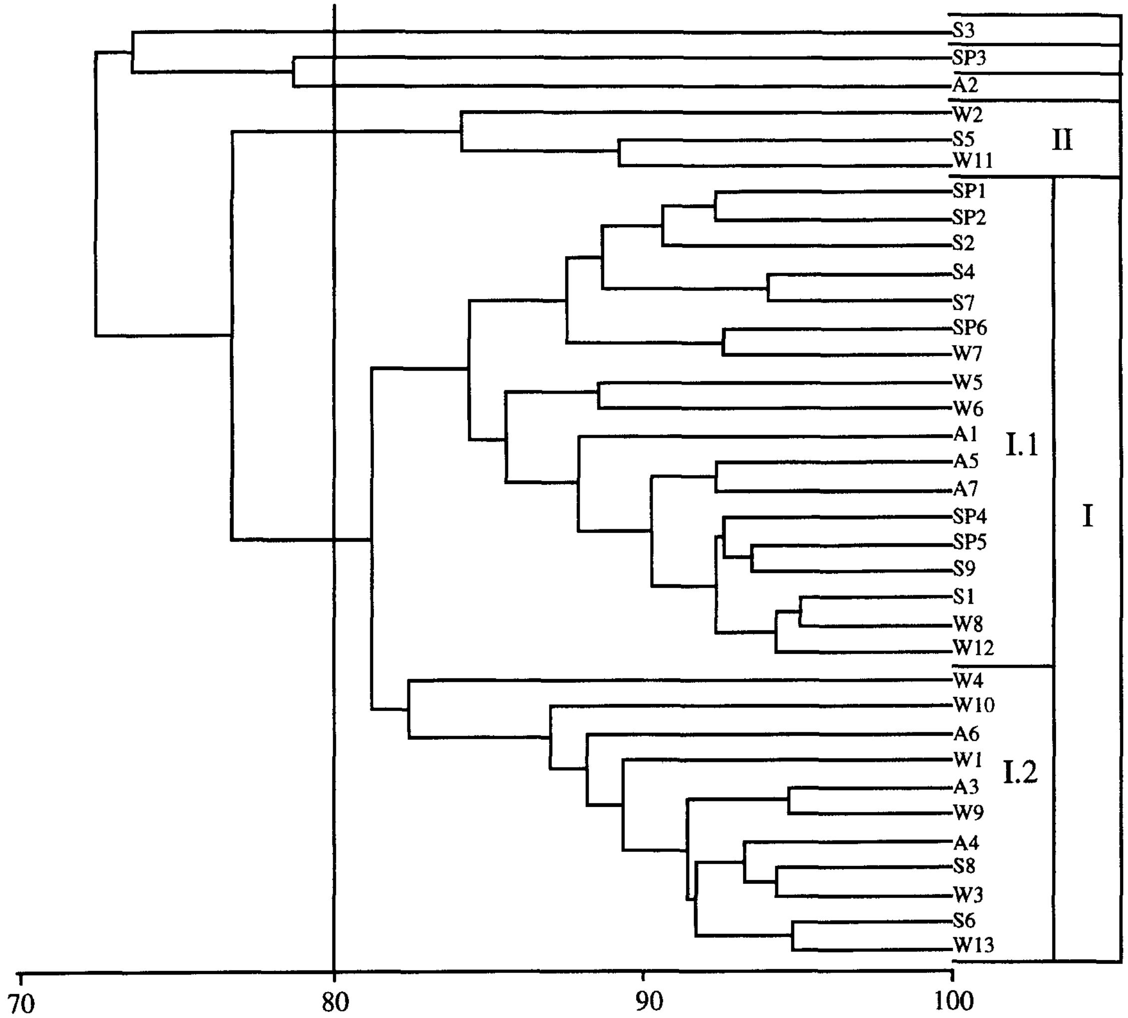

Fig. 3 Dendrogram for group-average clustering of Bray-Curtis similarity between 35 *Callianassa filholi* burrows from four different seasons. (Sp = spring; S = summer; A = autumn; and W = winter.)

which were almost spherical in shape, occurred equidistantly along the burrow system, with the exception of a relatively long shaft which connected the upper part of the burrow to a lower, generally horizontal region. The number of turning chambers varied from 4 to 14 (mean/SD = 8.3/2.7) and chambers did not necessarily signify a change in burrow direction or a side branch. The number of dead ending side branches varied between 1 and 5 (mean/SD = 2.5/1.2) of which up to three were terminated by turning chambers. Some burrows (31%) contained sumps (s), which were found in the lower part of the burrow and were at the dead end of one or two side branches. Maximum depth and lateral extent varied greatly between burrows, ranging from 10 to 65.5 cm (mean/SD = 24.1/10.5 cm) and from 9 to 112.8 cm (mean/SD = 36/19.3 cm), respectively. Similarly, the total length of the burrow system varied between 19.9 and 121 cm (mean/SD = 57.2/22.9 cm), with a corresponding burrow volume between 8 and 675.3 cm^3 (mean/SD = 123/121 cm^3).

Mulitvariate analysis

One-way ANOSIM permutations to test between pairwise combinations revealed that there were no significant differences in burrow morphology between spring, summer, autumn, and winter (Global R = 0.095, significance level = 6.8%). Cluster analysis of the burrow data distinguished two separate groups and three individual burrows at a similarity level of 80%. Within Group 1, a further two subgroups could be identified at a slightly higher similarity level (82%) (Fig. 3). Burrows from different seasons were present in each grouping and the three individual burrows represented casts taken in spring, summer, and autumn. Analysis of burrow

Table 1 Mean size (cm^3 and cm, respectively) and dissimilarity (DS) of *Callianassa filholi* burrow features averaged for and between seasons for each combination as calculated by SIMPER. Burrow features are ranked in order of their percentage contribution ($\delta i\%$) to the average Bray-Curtis dissimilarity between seasonal combinations, including the ratio ($\delta i/SD_{\delta i}$) and expressed as cumulative percentage ($\Sigma\delta i\%$) (cut-off to features list applied at 50%) (maximum values indicated in bold).

	Average size		$\delta i\%$	Ratio	$\Sigma\delta i\%$
DS = 17.61%	Spring	Summer			
Volume	**188**	156	28.98	1.39	28.98
Lateral extent	**52.8**	37.5	9.38	1.22	38.36
Total length	**73.4**	63.6	8.17	1.16	46.53
DS = 18.11%	Summer	Autumn			
Volume	**156**	123.1	28.31	1.29	28.31
Length of shafts	**5.2**	4.9	7.77	1.43	36.08
Total length	**63.6**	60.8	7.54	1.18	43.62
DS = 19.15%	Autumn	Winter			
Volume	**123.1**	69.9	25.84	1.53	25.84
Total length	**60.8**	42.6	10.28	1.49	36.12
Lateral extent	**40.2**	24.9	9.86	1.59	45.97
DS = 21.07%	Winter	Spring			
Volume	69.9	**188**	27.97	1.59	27.97
Lateral extent	24.9	**52.8**	11.53	1.4	39.5
DS = 18.47%	Spring	Autumn			
Volume	**188**	123.1	24.92	1.43	24.92
Lateral extent	**52.8**	40.2	8.83	1.24	33.75
Length of shafts	4.2	**4.9**	7.08	1.42	40.83
Total length	**73.4**	60.8	6.86	1.31	47.69
DS = 19.22%	Summer	Winter			
Volume	**156**	69.9	26.23	1.09	26.23
Total length	**63.6**	42.6	11.41	1.52	37.63
Lateral extent	**37.5**	24.9	8.96	1.55	46.6

Table 2 Results of linear regressions between environmental variables and *Callianassa filholi* burrow features (significant values in bold).

	Sediment grain size			Organic content		
	F	*P*	r^2	*F*	*P*	r^2
Lateral extent	0.072	0.7897	0.00	11.4	**0.0019**	0.26
Total length	0.073	0.7888	0.00	10.5	**0.0027**	0.24
Volume	3.17	0.0848	0.09	2.77	0.1054	0.08
	Seawater temperature			**Shore height**		
	F	*P*	r^2	*F*	*P*	r^2
Lateral extent	1.32	0.2585	0.04	4	0.0547	0.09
Total length	4.21	**0.0481**	0.11	2.88	0.1001	0.09
Volume	1.75	0.1955	0.05	2.3	0.14	0.04

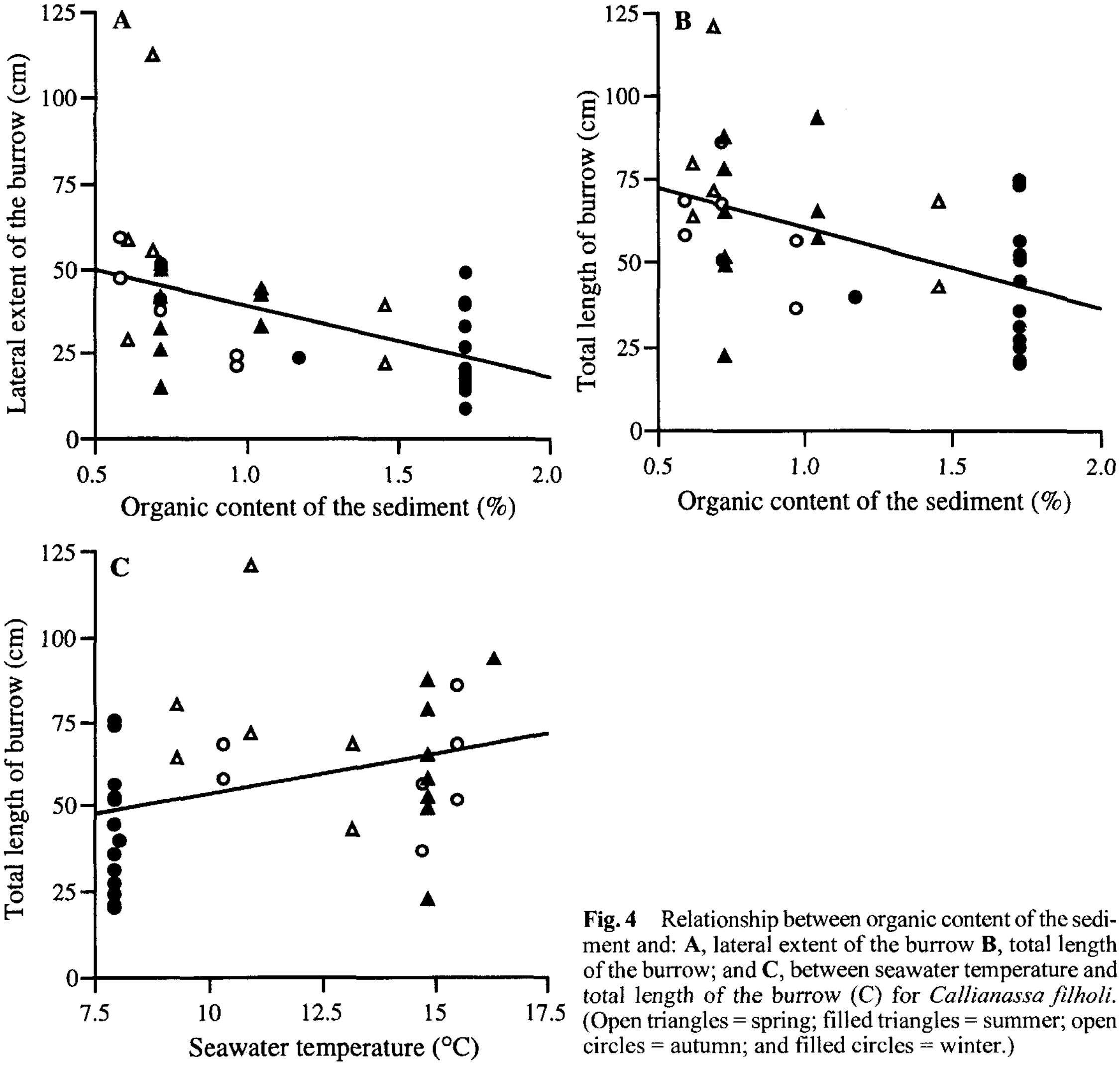

Fig. 4 Relationship between organic content of the sediment and: A, lateral extent of the burrow B, total length of the burrow; and C, between seawater temperature and total length of the burrow (C) for *Callianassa filholi*. (Open triangles = spring; filled triangles = summer; open circles = autumn; and filled circles = winter.)

features between seasons in pairwise combinations using SIMPER identified dissimilarities of 17.61–21.07% for all combinations (Table 1). Three burrow features contributed to 50% of the dissimilarities (indicated by consistently high ratio values); these were lateral extent, total length, and volume of the burrow. All three size parameters showed highest values in spring, and decreased over summer and autumn to lowest values in winter. Linear regressions for each of the three size parameters and measured environmental variables showed no significant relationship between sediment grain size and shore height respectively (Table 2). In contrast, there was a significant linear relationship between organic content and both lateral extent and total length of the burrow, and between seawater temperature and total length of the burrow (Fig. 4).

DISCUSSION

Resin casts of *C. filholi* burrows reveal a morphology similar to that of other callianassid species. Callianassid burrows usually comprise horizontal tunnels and vertical shafts which are connected by bulbous turning chambers. Access to the sediment surface is provided by several vertical openings, which are either wide inhalant or narrow exhalant shafts (Nickell & Atkinson 1995). The latter are characterised by an exhalant nodule at the base, which is used by the inhabiting shrimp to expel fine sediment, which forms conspicuous mounds at the sediment surface (Stamhuis et al. 1996). Coarse and unwanted material might be stored in sumps, which are dilated, dead ending branches in the lower part of the burrow (Atkinson & Nash 1990).

The burrow morphology of *C. filholi* is in general comparatively simple, and most closely resembles that of *Nihonotrypaea harmandi* which has a central system of oblique shafts and bulbous chambers descending into the sediment. However, burrows of *N. harmandi* possess two identical connections to the surface and show little horizontal extension (Tamaki & Ueno 1998), whereas *C. filholi* burrows comprise vertical openings which are distinctively either wide inhalant or narrow exhalant shafts. Furthermore, burrows of *C. filholi* have a number of horizontal tunnels and chambers, and the horizontal extension between openings in the upper part of the burrow is similar to that observed in *Neotrypaea californiensis* burrows (Swinbanks & Murray 1981). Therefore, despite the general callianassid similarities, burrows of *C. filholi* seem to display a species-specific morphology.

Callianassa filholi burrows also exhibit some intraspecific plasticity over time. Although morphological differences were not statistically significant, SIMPER identified a degree of dissimilarity (17–20%) between burrows from different seasons. Observed dissimilarities were predominantly linked to lateral extent, total length, and volume of the burrow. Each size parameter showed the highest value in spring and declined to minimum values in winter. Total length of the burrow was significantly related to seawater temperature and decreased to a minimum in winter when seawater temperature was low (7.9°C). It has been reported for temperate callianassid species that sediment turnover activity varies with season (Posey 1985; Swinbanks & Luternauer 1987). In particular, *C. subterranea* has been recorded to be virtually inactive at low temperatures (<7°C, Rowden et al. 1998), and low sediment expulsion activity of *C. filholi* is significantly related to minimum seawater temperature in colder months (~7°C, Berkenbusch & Rowden 1999). As sediment reworking by deposit-feeding callianassids is intrinsically linked to burrow maintenance and feeding (Stamhuis et al. 1997), it is likely that low sediment turnover rates are reflected in smaller-sized burrows during colder months. Low values for total length of *C. filholi* burrows in winter support this contention.

The significant relationship between both lateral extent and total length of the burrow and organic content of the sediment showed that burrows were smaller in winter when organic content of the sediment was high. A link between burrow morphology and organic content of the sediment has been suggested for subtidal *C. subterranea* populations, which appeared to construct burrows that are more shallow and complex in sediments with low organic content than in organically rich mud (Nickell & Atkinson 1995; Rowden & Jones 1995). Rowden & Jones (1995) reasoned that to meet its energetic requirements the deposit-feeding callianassid needs to process higher amounts of sediment, resulting in more complex burrows in organically poor sediments, than in enriched substrata. Alternatively, Stamhuis et al. (1997) suggested that higher competition for food and space induces shrimp to construct deeper burrows in organic rich sediments. Reasoning that as the abundance of benthic fauna in the sediment surface has been found to increase with organic content (Creutzberg et al. 1984), *Callianassa subterranea* avoids competition with shallow burrowing infauna by constructing relatively deep burrows. Deep burrows in turn result in fewer openings to the surface (i.e., less complex), as a result of the increased effort to maintain openings in deep as opposed to shallow burrows (Stamhuis et al. 1997). Spatial competition has also been suggested to influence burrow morphology for an intertidal *Biffarius arenosus* population; spiral sections featured in some burrows and possibly reflect the necessity to exploit most of the food supply in a given area (Bird & Poore 1999).

It appears unlikely for the intertidal *C. filholi* population that observed seasonal differences in burrow morphology are associated with such competition for food or space. Abundances of macroinfauna are generally low in sandy intertidal environments and the low shrimp population density, which did not show any significant changes over time (16 shrimp m^{-2}, Berkenbusch & Rowden 1998), implies that competition is unlikely to influence plasticity of *C. filholi* burrows. As low values for all three size parameters coincided with both low seawater temperature and relatively high organic content of the sediment, it is probable that either, or the combination of both environmental factors influence the burrow morphology. As there was no statistically significant difference in mean organic content between seasons (F-test, $F = 5.1$; $P > 0.05$), but a strong link between the shrimp's sediment turnover activity and temperature (Berkenbusch & Rowden 1999), it is likely that the observed intraspecific variation in burrow morphology is related to seasonal changes in seawater temperature. However, this interpretation is confounded by the relationship between burrow size and organic content, and to provide unambiguous results, it is obviously necessary in the future to investigate the influence of both factors on burrow morphology independently.

A comparative study of intertidal populations of *N. californiensis* and *Neotrypaea gigas* in muddy and sandy sediments related differences in burrow morphology to a combination of environmental factors i.e., sediment type and tidal height/exposure (Griffis & Chavez 1988). In the present study, however, dissimilarities between *C. filholi* burrows were not significantly related to either sediment grain size or shore height. Nevertheless, the importance of such environmental conditions might be dependent on their relative magnitude, for example neither mean sediment grain size nor shore height varied considerably at the study site (2.32–2.41 phi and 74–185 m horizontal shore distance—that is approximately mean low water spring and mean low water neap), as well as on the thalassinidean species concerned.

Since detailed studies have revealed high levels of variation in burrow morphology for a number of thalassinidean species (see Dworschak 1983), interspecific differences have been associated with the feeding mode of the inhabitant shrimp (Suchanek 1985; Vaugelas 1990; Griffis & Suchanek 1991). Such models based on different trophic modes between species provide a general burrow classification scheme and highlight distinct differences in burrow morphology e.g., between callianassids and upogebiids. At the same time, identification of particular burrow features in relation to feeding strategies accounts for trophic adaptations in relation to a dynamic environment (Nickell & Atkinson 1995). However, models based on feeding strategies do not suffice to explain intraspecific variation in burrow morphology and it is evident that other more potentially enlightening explanations need to be considered and examined. It has been suggested that species-specific burrows represent morphological features analogous to those used in thalassinidean taxonomy; thus, the interspecific variation in thalassinidean burrows is a result of phylogenetic affinities and ecological adaptations of each species (Dworschak & Ott 1993). Whereas ecological adaptations to a similar environment might result in some similarities in particular burrow features between species, intraspecific burrow plasticity is probably related to prevailing environmental conditions. Although the present study has linked variation in the burrow morphology of *C. filholi* to seawater temperature/sediment organic content, it has also highlighted the need for future research to focus on intraspecific burrow plasticity for both intertidal and subtidal species, in relation to environmental conditions and biological factors. In this respect, we suggest that the following themes warrant future investigation concerning the relationship between burrow sharing/number of shrimp per burrow and burrow morphology: the relative importance of seawater temperature in relation to significant differences in food availability; and the effect of physical disturbance on burrow structure such as experienced predictably on open sandy beaches.

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Appendix 1 Burrow measurements of *Callianassa filholi* burrows determined from resin casts at Otakou. (Sp = spring; S = summer; A = autumn; W = winter.)

	Burrow number														
Burrow measurements	SP1	SP2	SP3	SP4	SP5	SP6	S1	S2	S3	S4	S5	S6	S7	S8	S9
Max. depth of burrow (cm)	24.2	21.6	23.1	19.7	31.9	20.2	25.4	35.2	65.5	22.0	11.4	21.8	42.7	27.8	35.6
Horizontal depth of junction (cm)					12.1	5.6	16.5	9.3	4.3	8.4	1.8		7.8		6.9
No. of inhalant openings	1	1		1	1	1	1	1	1	2	1	1	1		1
No. of exhalant openings	2	1	1	1	2	2	1	1	1	3	1	1	1	1	1
Length inhalant shaft (cm)	4.5	4.9		8.0	12.1	4.5		7.7	8.5	6.6	3.0	8.6	8.1		3.5
Length exhalant shaft (cm)	4.5		2.6		6.2	5.4	11.8	10.7	5.5	7.9				8.0	5.7
Diam. of inhalant shaft (cm)		1.4		1.2	0.9	1.1	1.2	1.1	1.1	1.2	0.4	0.4	1.2		0.6
Diam. of exhalant shaft (cm)	0.5		0.5		0.5	0.4	0.4	0.4	0.4	0.5		0.4		0.5	0.3
Length exhalant nodule (cm)	2.5		2.8	3.9	2.5	1.7	2.9	2.6	2.4	2.6	1.1		2.3	2.0	2.2
Width exhalant nodule (cm)	1.3		1.5	1.7	1.3	0.8	1.2	1.1	1.4	1.3	0.6		1.0	0.7	0.9
Height exhalant nodule (cm)	1.2		1.3	1.4	1.6	1.0	1.5	1.3	1.6	1.8	0.6		1.1		1.2
Length of tunnels (cm)	1.7	2.4	4.6	1.7	2.1	1.9	2.1	1.5	4.4	1.8	0.9	2.6	1.7	1.4	1.8
Diam. of tunnels (cm)	1.2	1.4	1.6	1.1	1.3	1.0	1.2	0.8	2.0	1.1	0.5	0.9	1.1	1.0	0.7
Length of shafts (cm)	2.5	3.7		8.8	5.2	5.2	4.3	1.1	12.4	1.9	1.3	11.0	3.6	2.6	9.0
Diam. of shaft (cm)	1.1	1.5		1.1	1.3	0.9	1.3	1.6	1.6	0.9	0.7	0.9	1.3	1.0	1.0
No. of turning chambers	7	12	13	13	8	6	9	8	13	10	10	5	14	9	7
Length of turning chambers (cm)	2.6	3.0	3.2	2.3	2.9	2.7	2.7	3.5	3.9	2.5	1.3	1.9	2.5	2.0	2.3
Width of turning chambers (cm)	2.7	2.8	2.8	2.0	3.2	2.8	2.4	3.5	4.0	2.7	1.3	1.9	2.7	2.1	2.4
Height of turning chambers (cm)	2.5	2.6	2.2	1.4	2.7	2.7	2.1	2.8	3.4	2.3	1.1	1.6	2.2	1.7	1.9
No. of turning chamber insections	6	11	11	12	7	1	8	7	12	9	9	4	10	8	6
No. of terminal turning chambers		1	1		2		2	2	3	1	1		1	1	
No. of dead ends	2	3	5	2	2	1	4	2	4	2	2	4	5	3	5
Lateral extent (cm)	29.2	58.1	112.8	54.9	39.7	21.8	44.4	33.4	42.6	49.5	15.3	32.6	51.3	25.9	42.1
Total length of burrow (cm)	64.3	80.0	121.0	71.7	68.5	43.0	65.1	57.8	93.9	87.5	22.3	52.3	65.6	49.5	78.3
No. of sumps	1.0	1.0	1.0			1.0		1.0		2.0			2.0		
Length of sumps (cm)	5.7	2.2	5.6			1.5		5.5		3.4			3.1		
Width of sumps (cm)	2.4	1.7	1.7			1.8		2.5		1.8			2.0		
Height of sumps (cm)	2.1	1.7	1.7			1.7		1.9		1.9			1.8		
Volume (cm^3)	243.4	247.1	320.8	91.9	89.6	135.2	134.1	187.3	672.4	96.9	21.3	39.3	91.6	62.1	98.8

Appendix 1 (*continued*)

	Burrow number																			
Burrow measurements	A1	A2	A3	A4	A5	A6	A7	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10	W11	W12	W13
Max. depth of burrow (cm)	19.0	14.4	19.5	24.3	35.0	21.4	34.2	16.8	15.4	29.1	17.1	15.6	10.0	28.0	20.5	28.5	15.1	11.2	19.5	20.7
Horizontal depth of junction (cm)	12.1	12.4	12.3	11.0	8.5	8.6		8.1	10.3	11.0	8.6	9.0	9.2	9.7	6.2	13.0	7.6	7.0	2.4	7.9
No. of inhalant openings	1	1	1	2	1		1	1	1	1		2		1	1	1	1	1	1	
No. of exhalant openings	1	2	1	1	1	1	1	1	1	1	1	3	1	1	2	1	2	1	2	1
Length of inhalant shaft (cm)	11.1			6.9				6.0	1.2			7.3		9.5	6.2		4.9	1.7	10.2	
Length of exhalant shaft (cm)		11.1	11.8	10.3	7.2	8.6	10.1	6.3	8.9	9.3	8.6	7.8	9.2	9.7		11.5			2.4	9.0
Diam. of inhalant shaft (cm)	1.2	1.0		1.1	0.6		1.4	1.0	1.0	1.0		1.2		1.1	1.1			0.7	1.2	0.4
Diam. of exhalant shaft (cm)	0.6	0.5	0.4	0.5	1.1	0.2	0.6	0.6	0.6	0.4	0.4	0.5	0.7	0.4	0.5	0.4			0.6	0.4
Length exhalant nodule (cm)	1.9	2.4	1.6	2.8	2.2	1.1		2.8	1.8		1.7	2.0	2.5	2.0	2.1	1.7	1.5	1.1	2.7	1.7
Width exhalant nodule (cm)	1.1	1.4	1.0	1.3	1.5	0.6		1.2	1.1		0.6	1.3	1.5	1.2	1.4	1.2	0.9	0.6	1.5	1.1
Height exhalant nodule (cm)	1.3	1.6	1.1	1.0	1.7	0.5		1.4	1.3		0.4	1.4	1.9	1.3	1.4	1.0	1.0	0.6	1.6	1.2
Length of tunnels (cm)	1.5	1.8	1.4	2.2	18.7	1.9	2.7	2.8	1.3	3.3	1.4	1.4	3.3	2.4	2.0	1.3	1.1	0.7	2.7	2.1
Diam. of tunnels (cm)	1.3	1.1	0.8	1.2	1.6	0.5	1.4	1.1	1.0	1.0	0.8	1.1	1.5	1.1	1.2	1.0	0.7	0.6	1.3	1.0
Length of shafts (cm)			3.7	1.9	5.2	1.2	22.3		1.6	1.6		1.3		3.2	2.8	1.6	1.0	0.4	2.7	6.8
Diam. of shaft (cm)			0.7	1.1	1.4	0.6	1.4		1.8	1.1		1.3		1.0	1.2	1.0	0.7	0.6	1.3	1.0
No. of turning chambers	10	10	7	5	7	10	8	5	5	7	5	6	4	7	11	7	11	9	7	4
Length of turning chambers (cm)	2.8	2.7	1.6	2.2	2.8	1.3	3.0	2.5	2.3	2.4	1.7	2.6	2.9	2.5	2.5	2.1	2.0	1.2	2.5	2.5
Width of turning chambers (cm)	3.2	2.9	1.7	2.7	2.9	1.2	2.9	2.2	2.2	2.5	1.9	2.7	2.7	2.6	2.4	2.2	1.8	1.3	2.5	2.3
Height of turning chambers (cm)	2.6	2.7	1.7	2.0	2.4	1.0	2.4	1.7	2.0	1.9	0.8	2.3	2.2	2.2	1.9	2.5	1.5	1.0	2.4	1.7
No. of turning chamber insections	9	5	6	4	6	10	7	4	4	6	4	5	3	6	10	6	9	8	6	3
No. of terminal turning chambers	2	2							1	1		1	2	1	1					
No. of dead ends	2	3	2	4	3	4	3	3	2	3	1	1	2	1	1	1	3	1	1	3
Lateral extent (cm)	47.3	58.8	21.0	24.9	40.7	37.9	51.0	40.3	9.0	33.2	18.8	15.1	26.9	15.7	49.2	20.4	17.5	14.4	39.1	24.0
Total length of burrow (cm)	58.5	68.4	36.5	56.5	68.2	51.5	86.2	52.6	21.0	51.5	27.4	56.9	36.1	44.6	75.2	31.1	24.3	19.9	73.8	39.8
No. of sumps		1.0							1.0					1.0				1.0		
Length of sumps (cm)		4.2							3.7					2.6				1.6		
Width of sumps (cm)		1.6							1.9					1.8				0.9		
Height of sumps (cm)		1.5							2.1					1.7				0.7		
Volume (cm^3)	210.7	165.8	41.4	64.8	195.0	18.0	165.9	35.9	39.1	36.7	8.0	118.7	112.2	111.5	145.4	48.1	69.3	24.3	122.7	36.8