Extraordinarily high earthworm abundance in deposits of marine macrodetritus along two semi-arid beaches

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ABSTRACT: Earthworms are common in most soil profiles; however, the abundance of earthworms varies greatly among habitats. The euryhaline earthworm *Pontodrilus litoralis* was recorded in extraordinarily high numbers in wrack material deposited on arid beaches along the western Australian coastline. Based on worm abundance in $20 \times 20 \times 20$ cm plots, we estimated worm densities to be as high as 4875 m^{-2} at one site. Mean (±SE) worm density was 3200 ± 466 m^{-2} for the north Leeman site, with a minimum density of 750 m^{-2} at the Point Louise site (1940 ± 475 m^{-2}). Using estimates of consumption by earthworms from previous research, we calculated that earthworms could consume approximately 19 kg m^{-2} yr^{-1} of wrack material deposited at Point Louise and 31 kg m^{-2} yr^{-1} at north Leeman. The densities and associated potential consumption rates of worms recorded in the wrack habitat well exceed any records of worm populations in other natural systems. The only similar estimates are those from artificially created habitats, such as manure heaps. Stable isotope analyses suggest that the earthworms (mean δ^{13}C –15.9 and δ^{15}N 6.9) were consuming the more ephemeral algal component (mean δ^{13}C –21.5 and δ^{15}N 3.7) of the wrack in preference to the more persistent seagrass material (mean δ^{13}C –12.4 and δ^{15}N 2.1). The extraordinary densities of earthworms in wrack habitat have implications for the rate of wrack turnover along beach habitats and incorporation of marine-derived nutrients into what is essentially a nutrient-poor terrestrial coastal system. High earthworm densities in the wrack also indicate that wrack as a habitat is a potential hotspot for diversity and metabolism, probably exceeding records for other more stereotypically rich habitats, such as rainforests.

KEY WORDS: Coastal systems · Detached macrophytes · Land–water interface · Nutrient turnover · Wrack

INTRODUCTION

Earthworms are one of the most important faunal groups in soil ecosystems because of their influence on soil formation, soil texture and nutrient recycling (Parmelee et al. 1998). These invertebrates are important for fragmentation and redistribution of plant material (Lee 1985, Tian et al. 1995) and for the excretion of nutrient-rich faeces (Lavelle 1988). As such, earthworms are invaluable in the decomposition process, particularly where large piles of organic matter accumulate.

Earthworms are common in most soil profiles; however, the abundance of earthworms varies greatly among habitats (Whalen 2004), with higher earthworm populations associated with plant litter comprising faster decomposing species (Tian et al. 1995). Estimates of earthworm numbers in soils range from 11 m^{-2} in a conventional orchard to 310 m^{-2} in pastures (Paoletti 1999), and up to 480 m^{-2} in a deciduous forest

(Whalen 2004). All of these habitats are systems where high earthworm abundances are expected. In contrast, high earthworm abundance on an arid beach environment does seem unusual, particularly in association with marine-derived materials.

Marine macrodetritus that accumulates along beaches, commonly referred to as wrack, may be an important component of the flow of nutrients that occurs from marine to terrestrial systems. Around the world, beaches can accumulate sizeable stocks of this marine debris, which includes organic matter such as macrophytes (macroalgae and seagrass), driftwood and carrion. Marine debris is washed ashore during storm events and heavy swells (Kirkman & Kendrick 1997). Wrack can be locally redistributed through wind and wave action, washing up in some areas of the beach and remaining absent from others. As such, wrack deposits are highly dynamic and heterogenous, and the size and nature of deposits can differ greatly over space and time (e.g. Ochieng & Erftemeijer 1999, Wells 2002). Hence, wrack deposits have the potential to provide a rich, yet highly dynamic habitat for a range of organisms, as is evident by the very high metabolic rates exhibited by beach-cast materials (Coupland et al. 2007).

The small euryhaline earthworm *Pontodrilus litoralis* (Grube 1855) is a cosmopolitan species widely distributed in warm beaches throughout the world (Blakemore 2002) (Afrotropical, Australian, Nearctic, Neo-

tropical, Oriental, Palaearctic regions and other coastal sites see the Australian faunal directory at: www.environment.gov.au/biodiversity/abrs/online-resources/fauna/afd/index. html). Unlike most earthworms, this species does not die when immersed in seawater, but within a few moments is able to relax and burrow within the sediment (Lee 1969). Due to this adaptive behaviour, Lee (1969, 1985) speculated that the species is dispersed by ocean currents. As such, this earthworm is ideally suited to using beach-cast materials.

The aims of this study were to: (1) document the abundance of the cosmopolitan earthworm *Pontodrilus litoralis* in beach wrack material from an arid western Australian beach; and (2) assess the importance of earthworm feeding activity to the decomposition and redistribution of beach-cast material into the terrestrial food web based upon stable isotope analysis and estimates of earthworm consumption of beach-cast material.

MATERIALS AND METHODS

Pontodrilus litoralis abundance was assessed along 2 semi-arid beach habitats on the west coast of Australia in May 2005 (Point Louise, 30° 02.927′ S, 114° 57.310′ E; north of Leeman, 29° 53.789′ S, 114° 58.756′ E) (Fig. 1). Tidal range across the region is slight, with the maximum range rarely greater than
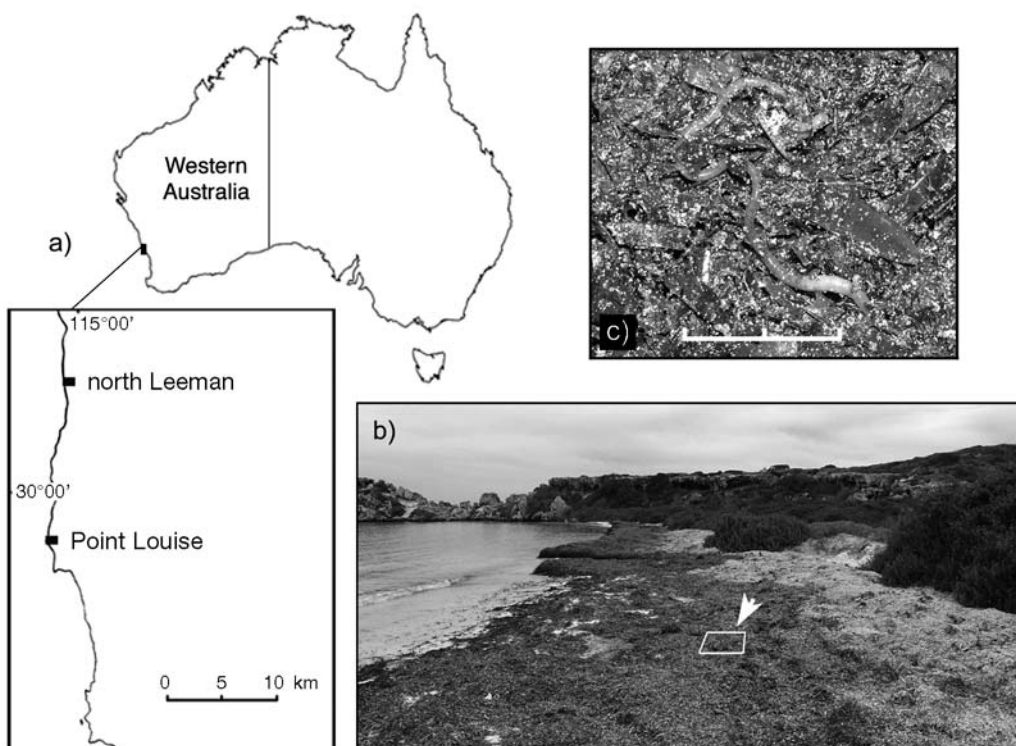

Fig. 1. (a) Location of the Point Louise and north Leeman study sites examined. (b) Beach at Point Louise with wrack deposits. Arrow and quadrat indicate approximate location of sampling; maximum distance from water to terrestrial vegetation is approximately 6 m. (c) *Pontodrilus litoralis in situ*. Scale bar = 3 cm

0.7 m, although there are distinct semi-diurnal tides (Hodgkin & DiLollo 1958). The climate of the region is semi-arid, and terrestrial habitat adjacent to the beaches is characterised by nutrient-poor sandy soils. The low productivity terrestrial system abuts highly productive marine habitats dominated by mixed-seagrass beds and macroalgal communities (Kirkman & Walker 1989, Walker 2000, 2003).

Large wrack deposits accumulate on the beaches at both sites (G. T. Coupland pers. obs.). Deposits may sit for many months, forming a layer up to 60 cm deep at the most landward side of the beach. The landward extent of the deposits can be up to 8 m from the swash zone. At the swash zone, the wrack deposits are frequently inundated with seawater and can be up to 110 cm deep. Fresh wrack material at the front of the wrack deposits consisted of a mixture of algae and seagrass macrodetritus. The older wrack material persisting towards the landward edge of the beach consisted mainly of seagrass material (*Amphibolis* and *Posidonia* species). When the top dry layer of wrack was removed (approximately 5 cm of dried seagrass), the wrack below was moist and had been broken down into considerably smaller particles (mean size < 5 mm). At a depth of 20 cm, the wrack material was like the soil of well-composted leaf litter. Below this soil layer was the sand characteristic of the beach habitat. There was little mixing of the composted material and sand.

To determine earthworm abundance, 8 plots of beach-cast wrack material, 20 × 20 × 20 cm in size, were excavated and the material placed in plastic bags at each site. Mean distance from the swash zone of the excavated regions was 5.4 m. Wrack material was sorted on site for earthworms. Worms from each plot were placed into separate plastic vials and transported on ice to the laboratory where they were frozen. Worms were rinsed in deionised water to remove all extraneous wrack material and dried in an oven at 55°C until they reached a constant weight. Whole worms from 3 plots at the Point Louise site were haphazardly selected for isotope analysis and ground to a fine homogenous powder in preparation for isotope analysis. The isotopic composition of the whole body of small invertebrates can be used to provide an insight into the animals' feeding ecology as food items are quickly assimilated into the body of the organism (DeNiro & Epstein 1978).

We used estimates of earthworm abundance to determine an approximate consumption rate (kg m^{-2} yr^{-1}) for earthworms in the wrack deposits, based on a conservative estimate of consumption by litter-feeding earthworms (earthworm feeding rate of 27 mg litter ind.$^{-1}$ d^{-1}; Satchell 1967). The diet of litter-feeding earthworms would be most similar to wrack-feeding earthworms. Satchell's (1967) calculation of earthworm feeding rates was determined using a range of earthworm feeding data from natural and agricultural systems (from earthworm feeding experiments by Franz & Leitenberger [1948] on *Corylus* leaf litter, van Rhee [1963] on alder and orchard leaves, and Needham [1957] on elm leaves; see Satchell's [1983] examination of earthworm ecology in forest soils). These feeding data were based mainly on *Lumbricus terrestris* L. and *L. rubellus* Hoffmeister. We compared the *Pontodrilus litoralis* wrack consumption rate with earthworm consumption rates reported in other habitats (Table 1).

Three replicates of each of the main components of wrack material at the Point Louise site were collected for isotope analysis (n = 3 for each species, except n = 2 for *Ulva compressa* Linnaeus [previously *Enteromorpha compressa*])*.* This included both seagrass and macroalgal species (seagrass species: *Amphibolis antarctica* [Labill.] Asch., *A. griffithii* [J. M. Black] Hartog, *Posidonia australis* Hook.f., *P. sinuosa* Cambridge and J. Kuo, *Syringodium isoetifolium* [Asch.] Dandy and *Halophila ovalis* [R. Br.] Hook.f.; algal species: *U. compressa*, *Ecklonia radiata* [C. Agardh] J. Agardh, *Sargassum linearifolium* [Turner] C. Agardh, *Sargassum* sp. and *Laurencia filiformis* [C. Agardh] Mont.). Decomposing mixed wrack material contained deep within the worm habitat was also collected for isotope analysis (n = 3 samples). Samples were placed in individual plastic bags and kept cool until return to the laboratory. Samples were rinsed in deionised water to remove any sand. Epiphytes were scraped off seagrass leaves using a razor blade. Whole seagrass leaves and blades for algae were dried in an oven at 55°C until they reached a constant weight. Samples of wrack were ground to a homogenous fine powder in preparation for isotope analysis.

Between 2.5 and 3.0 mg of worms and 5.0 and 5.5 mg of each wrack component were weighed and placed into tin capsules. Samples were then analysed for δ^{15}N and δ^{13}C. Capsules were combusted at 1000°C using PDZ Europa instruments (a Roboprep-preparation system interfaced with a Europa 20:20 continuous flow isotope ratio mass spectrometer [CFIRMS]). The analytical precision of the instruments was ±0.3‰ for δ^{15}N and ±0.2‰ for δ^{13}C. Isotope δ ratios are expressed in the δ-notation according to:

$$\delta\ (‰)\ =\ (R_{\text{sample}}/R_{\text{standard}}) \times 1000$$

where (‰) is δ^{13}C or δ^{15}N, and R_{sample} and R_{standard} are the ^{15}N:^{14}N or ^{13}C:^{12}C ratios of the samples or standard, respectively. Values for δ^{15}N are reported relative to atmospheric N$_2$ and for δ^{13}C are expressed relative to PeeDee Belemnite (PDB). Percentage composition (%)

of C and N was calculated for each potential wrack component during stable isotope analysis.

To characterise the potential diet of organisms, potential food sources must differ in $\delta^{13}C$. To determine whether sources differed in $\delta^{13}C$ and $\delta^{15}N$, a 1-way ANOVA was used to test the null hypotheses of no differences in $\delta^{13}C$ and $\delta^{15}N$ among potential earthworm food sources (seagrass, algae and decomposing wrack material) using JMP™ software. Probability levels were set at $p < 0.05$. Tukey's HSD test was then used to determine where differences between potential food sources occurred. IsoSource™ was also used to assess which of the wrack components were potentially contributing most to the *Pontodrilus litoralis* diet. Diet to tissue discrimination values used in the IsoSource™ analysis (enrichment of earthworm tissue relative to diet: 2‰ $\delta^{13}C$ and 4‰ $\delta^{15}N$) were based on isotopic values from a study on earthworm feeding ecology (Hendrix et al. 1999). The C:N ratios were calculated for each wrack component based on the percentage composition of C and N determined during stable isotope analysis.

RESULTS

Worm densities

In total, 621 earthworms from the species *Pontodrilus litoralis* were collected, with worms having a mean (±SE) length of 3.2 ± 0.2 cm. We calculated worm densities as high as 4875 m^{-2}, with Point Louise (mean ± SE = 1940 ± 475 m^{-2}, range = 750 to 4875 m^{-2}) exhibiting lower densities than the north Leeman site (3200 ± 466 m^{-2}, range = 925 to 4650 m^{-2}) (Fig. 2). Based on estimates of consumption by earthworms, we calculated that *P. litoralis* could consume approximately 19 kg m^{-2} yr^{-1} of the wrack material deposited at Point Louise and 31 kg m^{-2} yr^{-1} at the north Leeman site. Estimates of gross annual wrack flux (kg m^{-2} yr^{-1}, which takes into account losses due to decomposition of individual wrack components, but not advective losses as calculated as part of a larger study) indicated that wrack consumption by *P. litoralis* has the potential to account for large amounts (>35%) of the wrack flux at both sites (Fig. 3).

Table 1. Estimated consumption of organic matter (kg^{-1} m^{-2} yr^{-1}) by earthworms for various habitats based on mean numbers of worms reported for specific habitats and a standard earthworm consumption rate of 27 mg worm^{-1} d^{-1} reported by Satchell (1967). FSO stands for 'from surveys of '

| Habitat type	Mean no. worms m^{-2}	Consumption (kg m^{-2} yr^{-1})	Species of earthworm	Location	Source
Agricultural habitat					
Conventional orchard	11	0.1	Not specified	FSO 350 sites worldwide	Paoletti (1999)
Cultivated fields	88	0.9	Not specified	FSO 350 sites worldwide	Paoletti (1999)
Coppiced deciduous forest	111	1.1	Not specified	FSO 350 sites worldwide	Paoletti (1999)
Orchards	212	2.1	Not specified	FSO 350 sites worldwide	Paoletti (1999)
Organic orchard	259	2.6	Not specified	FSO 350 sites worldwide	Paoletti (1999)
Corn field	229	2.3	Includes *Allolobophora chlorotica, Aporrectodea longa, A. rosea, A. trapezoides, A. tuberculata, A. turgida, Dendrobaena octaedra, Lumbricus terrestris*	Québec, Canada	Whalen (2004)
Pastures	307	3.0	Not specified	FSO 350 sites worldwide	Paoletti (1999)
Hayfield	322	3.2	Includes *Aporrectodea rosea, A. turgida, Lumbricus castaneus, L. terrestris*	Québec, Canada	Whalen (2004)
Manure sludge	1520	15.0	Not specified	Surnadal, Norway	Hansen (1996)
Manure heap	4950	48.8	*Eisenia fetida*	Northwest Spain	Monroy et al. (2006)
Natural habitat					
Coniferous forests	51	0.5	Not specified	FSO 350 sites worldwide	Paoletti (1999)
Tropical and subtropical forest	76	0.7	Not specified	FSO 350 sites worldwide	Paoletti (1999)
Deciduous forests	134	1.3	Not specified	FSO 350 sites worldwide	Paoletti (1999)
Meadows	200	2.0	Not specified	FSO 350 sites worldwide	Paoletti (1999)
Grass savanna	202	2.0		Lamto, Côte d'Ivoire	Lavelle (1978)
Mixed deciduous forest	480	4.7	Includes *Allolobophora chlorotica, Aporrectodea longa, A. rosea, A. tuberculata, A. turgida, Lumbricus terrestris, Octolasion tyrtaeum*	Québec, Canada	Whalen (2004)
Beach wrack (Point Louise)	1941	19.1	*Pontodrilus litoralis*	Point Louise, Western Australia	Present study
Beach wrack (north Leeman)	3200	31.5	*Pontodrilus litoralis*	North Leeman, Western Australia	Present study
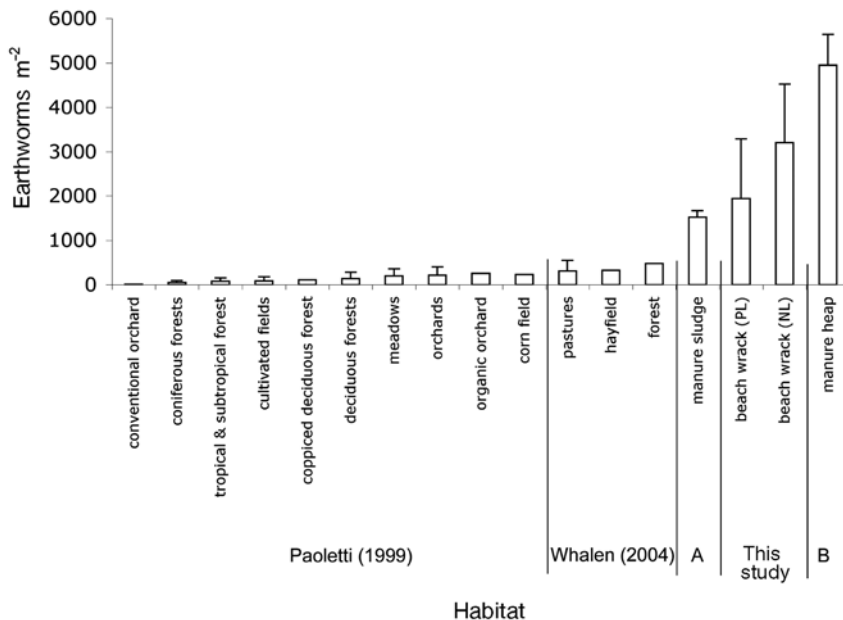
Fig. 2. Mean (±SD) earthworm densities from terrestrial habitats reported in the literature and from the arid beaches in this study (PL: Point Louise; NL: north Leeman). A: Hansen (1996), B: Monroy et al. (2006). Standard deviations are not recorded for some of the habitats as values were not provided

Stable isotopes and IsoSource™ modelling

Pontodrilus litoralis had a mean (±SE) δ^{13}C value of −15.9 ± 0.13 (range = −15.6 to −16.1; n = 3) and a mean δ^{15}N of 6.9 ± 0.04 (range = 6.9 to 7.0; n = 3) (Fig. 4). Potential earthworm food sources among the wrack material varied in natural isotope abundance, with macroalgal samples significantly depleted in δ^{13}C relative to seagrass species (macroalgae range = −24.0 to −18.0; seagrass range = −15.0 to −8.6; n = 3 for each species) ($F_{2,32}$ = 117.2, p < 0.0001) (Fig. 3). Macroalgae were significantly enriched in δ^{15}N compared with seagrass (macroalgae range = 1.8 to 8.0; seagrass range = 0.2 to 4.3; n = 3 for each species) ($F_{2,32}$ = 4.57, p = 0.018). Mixed decomposing wrack material was not significantly different in δ^{15}N to either the seagrass or algal material (mean δ^{15}N = 3.4 ± 0.15), but was significantly enriched in δ^{13}C (mean δ^{13}C = −12.3 ± 0.25) compared with the algae (Fig. 3). Decomposing wrack material was similar to seagrass in δ^{13}C as, unlike algae, seagrass is a persistent component of the wrack deposits and most of the decomposing material is probably remnant seagrass material (G. T. Coupland pers. obs.). According to the IsoSource™ model, algal and seagrass material were both likely to contribute to the diet of *P. litoralis*, particularly *Sargassum* sp. (67 to 87%), the mixed wrack material (6 to 28%) and *Amphibolis griffithii* (0 to 9%) (values are based on the 1st and 99th percentile range for the calculated feasi-

ble distributions in IsoSource™). Food preference exhibited by *P. litoralis*, according to the IsoSource™ analysis, did not correspond with the most abundant of the potential food items in the wrack, which was seagrass, specifically *Amphibolis*, at both sites (Table 2).

The C:N ratios varied considerably among wrack components. The algae *Ulva compressa* had a very high C:N ratio (high amount of carbon compared with nitrogen), while the algae *Laurencia filiformis* exhibited a low C:N ratio (Table 3). The long-lived seagrass species (*Amphibolis* and *Posidonia*) had higher C:N ratios than the shorter-lived *Halophila* and *Syringodium* species (Table 3).

DISCUSSION

The extraordinarily high earthworm densities recorded in beach wrack in this study were an order of magnitude greater than the highest densities reported from other natural habitats, even higher than recorded in the stereotypical rich and diverse forest habitats (e.g. 76 worms m⁻² in a tropical forest and 480 worms m⁻² in a deciduous forest; Whalen 2004) (Fig. 2). The only
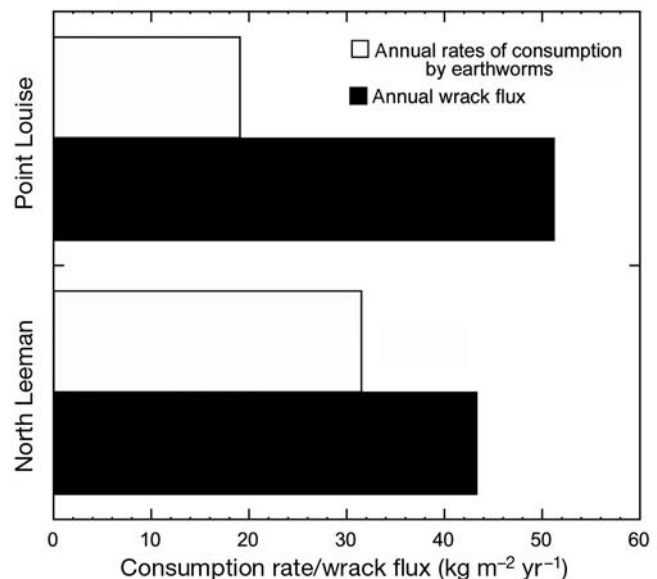

Fig. 3. *Pontodrilus litoralis.* Potential wrack consumption rates for the earthworm and estimates of mass flux of wrack from the Point Louise and north Leeman sites
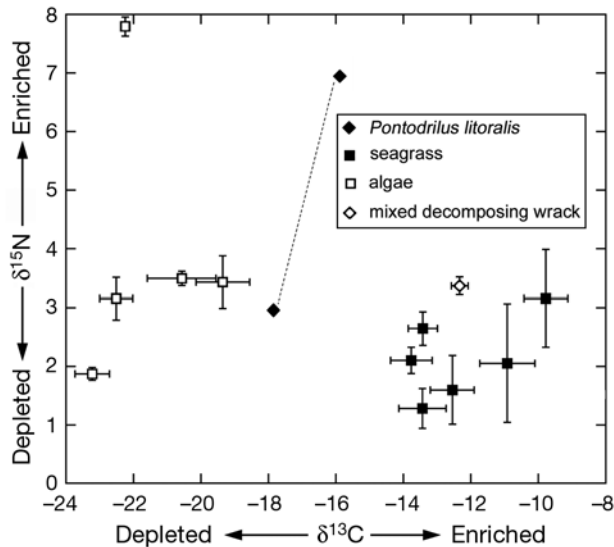
Fig. 4. Plot of δ^{13}C versus δ^{15}N for the wrack components (seagrass, macroalgae and mixed decomposing wrack) and the earthworm *Pontodrilus litoralis* tissues from the Point Louise beach habitat in Western Australia. Units are ‰ (±SE). Mean δ^{13}C and δ^{15}N values of the earthworm *P. litoralis* are in relation to the potential food sources, taking into account the trophic enrichment of 2 and 4‰ for δ^{13}C and δ^{15}N, respectively. The estimated trophic enrichment of carbon and nitrogen of earthworm tissues is illustrated by the dashed line

earthworm densities recorded higher than those in this study were reported from composting manure piles (Monroy et al. 2006) (Fig. 2), which is a highly rich yet artificially created habitat.

Given that earthworms were recorded in such high densities in beach wrack, the worms have the potential to turn over large amounts of the wrack material. Based on worm abundance from the literature (e.g. Lavelle 1978, Whalen 2004), we estimate that worms could consume up to 3.2 kg m^{-2} yr^{-1} of litter in a hayfield and up to 4 kg m^{-2} yr^{-1} of leaf litter in a forest system (Table 1). If the same consumption rate is applied to earthworms found in wrack deposits in western Australia (this study), then *Pontodrilus litoralis* could be expected to turn over up to 19 kg m^{-2} yr^{-1} of the wrack material deposited at Point Louise and up to 31 kg m^{-2} yr^{-1} at the north Leeman site if consistent feeding throughout the year is assumed (Table 1). The high predicted rates of wrack consumption by *P. litoralis* may account for over 35% of the gross annual wrack flux estimated for the sites investigated (Fig. 3). As such, earthworm feeding activity may be highly important to the decomposition and redistribution of beach-cast material.

Table 2. Wet weight composition (%) by type of wrack deposits at Point Louise and north Leeman sites in May 2005

Wrack type	Point Louise	North Leeman
Macroalgae		
Ecklonia radiata	0.7	0.6
Other Phaeophyta	1.1	16.3
Rhodophyta	1.0	19.5
Chlorophyta	0.5	2.4
Seagrass		
Posidonia	9.9	8.1
Amphibolis	85.0	52.4
Halophila and *Syringodium*	0.5	0.7
Other organics		
Driftwood, coral, other organic material	1.4	0.0

Besides direct consumption of wrack material, detrital consumers can increase the rate of decomposition of plant material by enhancing microbial growth (Jedrzejczak 2002a). Earthworm casts in particular contain more micro-organisms, inorganic material and organic matter in a form that is available to plants, than does soil (Ghabbour 1966). These casts contain enzymes that continue to breakdown organic matter even after they have been excreted by the worm (Ghabbour 1966). As such, the earthworms found in the wrack deposits are likely to be highly important bioturbators in beach habitats and consequently would be significant in incorporating marine-derived nutrients into the low productivity semi-arid coastal food web. Recruitment of numerous coastal plant seedlings in the top layer of the wrack observed at both sites exemplifies

Table 3. C:N ratios (mean ± SE) of potential earthworm food sources within the wrack deposits. Food sources with lower C:N ratios are considered more palatable to consumers. n = 3 for all species, except *Ulva compressa* (n = 2)

Food source	C:N ratio	Min. C:N	Max. C:N
Macroalgae			
Ulva compressa	36.7 ± 0.9	35.8	37.6
Sargassum linearifolium	34.3 ± 3.7	28.8	41.3
Ecklonia radiata	26.4 ± 2.9	21.1	30.9
Sargassum sp.	21.6 ± 1.7	18.3	23.9
Laurencia filiformis	12.2 ± 0.7	10.9	13.0
Mixed wrack			
Decomposing wrack material	26.3 ± 1.1	24.2	28.0
Seagrass			
Amphibolis griffithii	27.9 ± 1.0	26.7	29.9
Posidonia sinuosa	26.3 ± 2.3	22.4	30.4
Amphibolis antarctica	25.0 ± 1.5	22.9	27.9
Posidonia australis	22.4 ± 2.6	17.3	25.5
Syringodium isoetifolium	15.3 ± 0.9	13.8	16.8
Halophila ovalis	14.1 ± 0.5	13.2	15.0

the rich nature of the material below the wrack surface created by earthworm feeding and the continuing decomposition process facilitated by the worm casts.

The more ephemeral algal material in wrack deposits appears to be preferentially consumed by *Pontodrilus litoralis*, rather than the more persistent seagrass material (based on IsoSource™ modelling of wrack and earthworm natural isotope abundance; Fig. 4). This indicates that the earthworms were seeking out specific food items within the wrack, which were not necessarily based on abundance of specific wrack components, as seagrass was the most abundant of the wrack components at both sites (Table 2). According to previous studies, brown macroalgae, such as *Fucus* sp., *Ecklonia* and *Macrocystis*, is the wrack component preferentially selected as a food item by wrack-dwelling consumers, such as the amphipods *Talitrus saltator* (Montague 1808), *Allorchestes compressa* Dana and *Megalorchestia pugettensis* (Dana 1853) (Robertson & Lucas 1983, Adin & Riera 2003, Mews et al. 2006), even when invertebrates could chose from a range of wrack constituents (including red and green macroalgae and a range of seagrass species). Consequently, it was not surprising that the earthworms in this study also preferentially selected brown macro-algae *Sargassum* sp. over other more abundant wrack components. As the C:N ratios of seagrass and macroalgae in this study are similar, it is likely that not only does the nutritional quality of the food make *Sargassum* more palatable to the earthworms, but a combination of factors also contributes, including fragmentation of *Sargassum* in the wrack and the fast rate of decomposition of *Sargassum* compared with other wrack components such as seagrass. Seagrass has been reported to be unpalatable to many herbivorous/detritivorous macrofauna, due to its high structural fibre and phenolic content (Zapata & McMillan 1979, Thayer et al. 1984). While earthworm numbers have often been inversely related to phenolic levels (Satchell & Lowe 1967), both algae and seagrasses are known to have high phenolic contents (McMillan et al. 1980, Ragan & Glombitza 1986, Targett & Arnold 1998). Phenolic concentrates have, however, been shown to decrease in litter a few weeks after weathering (King & Heath 1967). As such, the phenols present in algal and seagrass wrack may be greatly reduced compared with the living tissue, and, hence, explain the palatability of the macroalgae and seagrass to *P. litoralis*. Palatability of food sources is also positively correlated with nitrogen content (Satchell & Lowe 1967). As such, the lower C:N ratio of *Sargassum* sp. compared with many of the other algal species supports the stable isotope results that indicate that *Sargassum* sp. is a preferred food source for the earthworm (as total nitrogen content can be used as a sub-

stitute for protein content). The similar C:N ratios, however, for many of the algal species compared with the seagrass are surprising given that macroalgae usually have lower C:N ratios than do the longer-lived seagrass species such as *Posidonia* and *Amphibolis* (Thayer et al. 1984).

Algal material in the wrack decomposes at a faster rate than does the seagrass material. As such, the bulk of wrack deposits that can remain *in situ* for many months, particularly to the landward edge of the beach, is largely composed of seagrass. Deposits are, however, often replenished with fresh wrack material following high tides and storm events. Hence, as long as the structural component of the wrack material (the slow decomposing seagrass component) remains on the beach to provide a habitat for the worms, the earthworms are able to persist on the beach in large numbers and consume the more palatable of the algal material when it is washed ashore.

Earthworms collected in this study were from wrack over 5 m from the swash zone. Hence, unlike the wrack located in the swash zone, wrack material at the 5 m distance was not freshly deposited. The length of time since deposition is important, as it has been demonstrated that wrack material must remain *in situ* for a sufficient time to allow colonisation by fauna (see studies by Inglis 1989, Jedrzejczak 2002b). The time since deposition of the wrack is important to the chemistry of the wrack deposits and the microflora that have been able to colonise them. Both these factors are influential in determining the faunal composition of wrack deposits (Jedrzejczak 2002b) and, hence, will have affected the densities of worms recorded in this study. Neither Inglis (1989) nor Jedrzejczak (2002b) recorded earthworms as macrofauna in their wrack faunal studies.

High abundance of earthworms supported by the wrack deposits demonstrates the rich food resource provided by wrack material. Earthworms are not the only invertebrates to use wrack accumulations and compete with other wrack inhabitants for the resource, as well as co-habiting with a range of invertebrate predators, such as spiders and rove beetles (G. T. Coupland pers. obs.). In fact, wrack accumulations are reported to be rapidly colonised by a wide variety of invertebrates. Initially, wrack is colonised by amphipods, adult Diptera and Coleoptera. After reaching their highest abundance after 3 d, these invertebrates are replaced in abundance by nematodes, turbellarians, enchytraeids, dipteran larvae and mites (Inglis 1989, Jedrzejczak 2002b). Thus, the earthworms reported in this study are amongst the second stage of wrack colonisers. Jedrzejczak (2002b) is the only study to our knowledge that records earthworm (oligochaete) colonisation of wrack, although the oligo-

chaetes reported in that study were meiofauna (0.1 to 1 mm) rather than macrofauna as reported in this study.

To the authors' knowledge, this is the first report of high densities of earthworms in beach habitats and represents the highest recorded densities for earthworms in any natural habitat. Wrack deposits provide an unusual, yet highly rich habitat for earthworms that can tolerate saltwater, as they are essentially piles of decomposing organic material. The extraordinary densities of these invertebrates suggest that the role earthworms play in the turnover of wrack material may be vitally important to the transfer of marine-derived nutrients to what is essentially a nutrient-poor terrestrial coastal system. The high earthworm densities in the wrack also indicate that wrack deposits are potential hotspots for diversity and metabolism, probably exceeding records for other more stereotypically rich habitats, such as tropical rainforests.

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