

Review

Arsenic bioaccumulation and species in marine Polychaeta

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Published whole tissue arsenic concentrations in polychaete species tissues range from 1.5–2739 µg arsenic/g dry mass. Higher mean total arsenic concentrations are found in deposit-feeding polychaetes relative to non-deposit-feeding polychaete species collected from the same locations. However, mean arsenic concentrations at some of the locations are skewed by the high arsenic concentrations of *Tharyx marioni*. There appears to be no direct correlation between sediment arsenic concentrations and polychaete arsenic concentrations. Arsenic bioaccumulation by polychaetes appears to be more controlled by the physiology of the polychaetes rather than exposure to arsenic via ingested material or the prevailing physiochemical conditions. Arsenic concentrations in polychaete tissues can vary greatly.

Most polychaete species contain the majority of their arsenic as arsenobetaine (57–98%), with trace concentrations of inorganic arsenic (<1%) and other simple methylated species (<7.5%). However, this is not always the case, with unusually high proportions of arsenite (57%), arsenate (23%) and dimethylarsinic acid (83–87%) in some polychaete species. Arsenobetaine is probably accumulated by polychaetes via organic food sources within the sediment. The presence of relatively high proportions of phosphate arsenoriboside (up to 12%) in some opportunistic omnivorous Nereididae polychaete species may be due to ingestion of macroalgae, benthic diatoms and/or phytoplankton.

Consideration of the ecology of individual polychaete species in terms of their habitat type, food preferences, physiology and exposure to arsenic species is needed for the assessment of arsenic uptake pathways and bioaccumulation of arsenic. Future research should collect a range of polychaete species from a wide variety of uncontaminated marine habitats to determine the influence of these ecological factors on total arsenic concentrations and species proportions. Copyright © 2005 John Wiley & Sons, Ltd.

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INTRODUCTION

Arsenic accumulation in the biota of uncontaminated marine ecosystems is naturally higher than that occurring in organisms inhabiting terrestrial environments.¹ Information on the biosynthesis and cycling of arsenic in uncontaminated marine environments will come from investigations that extend the range of organisms and habitats that have

so far been examined. Published scientific literature has not established the contributions of marine polychaetes to arsenic cycling in marine environments. Polychaetes belong to the phylum Annelida, the segmented worms.^{2–5} Over 20 000 species of polychaetes have been described, and they are classified into over 70 families.³ Polychaeta is a diverse animal class, its taxa occupying a wide range of marine habitats.^{2,3,5–7} Infaunal polychaete species are important for the ecological functioning of sediments and probably influence the 'fate' of arsenic through their foraging activities.^{2,8–12} In particular, polychaete sediment consumption and associated bioturbation facilitate redox and

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biologically mediated arsenic species transformations.^{10,11,13} These processes can directly influence the flux of arsenic from sediments into overlying seawater and its bioavailability to a suite of other marine organisms.^{10,11} The contribution of polychaetes to the marine food web as prey is appreciable and probably underestimated.^{2,14–18} Published marine food-chain arsenic biotransference and biomagnification investigations have rarely included polychaetes.^{11,19} Additionally, only a limited number of polychaete species (<22) have had their arsenic concentrations quantified (Table 1) and only six have had their arsenic species identified (Table 2).

The aim of this review is to provide a synthesis of published studies on arsenic concentrations and species proportions in polychaete tissues. Environmental exposure to arsenic species and factors affecting the accumulation of arsenic and specific arsenic species are discussed.

TOTAL ARSENIC CONCENTRATION IN POLYCHAETES

Published whole-tissue arsenic concentrations in polychaete species classified to three common feeding guilds, i.e. feeding preferences (opportunistic, raptorial, omnivorous scavengers and/or predators; deposit feeding omnivores; and suspension feeding omnivores), have a range of 1.5–2739 μg arsenic/g dry mass (Table 1). Higher mean total arsenic concentrations are found in deposit-feeding polychaetes relative to non-deposit-feeding polychaete species collected from the same location.^{13,20,23} However, mean arsenic concentrations in the Gibbs *et al.*²³ study were skewed by the high arsenic concentrations of *Tharyx marioni*. Whole-tissue total arsenic concentration variation among deposit-feeding polychaetes may be due to differences in particle selectivity, and differences in food item selectivity and inadvertent ingestion of sediments during feeding may account for the arsenic concentration differences between infaunal non-deposit-feeding polychaetes. Polychaete depuration, prior to analysis, to eliminate unassimilated arsenic compounds in digestive organs is important, especially when analysing infaunal deposit-feeding polychaete samples from contaminated benthic habitats.^{23,29,30} The need for periodic removal of faecal matter, thorough cleaning of depuration containers to avoid reingestion, and use of seawater from the location sampled during depuration has been noted.^{13,20} Various periods of depuration ranging from 0 to 7 days have been reported (Table 1) and may also add to the variability in arsenic concentrations reported. Removal of infaunal polychaetes from sediment and its associated redox conditions during depuration may have a similar effect to that of starvation, i.e. limiting arsenic uptake while arsenic excretion rates remained unaltered, causing arsenic concentrations to decrease. Alternatively, unassimilated ingested material that is not depurated may add to arsenic concentration. Depuration may be far more important when analysing polychaetes from contaminated environments, where the contribution of unassimilated arsenic from food and sediment

may be high enough to confound the accurate determination of assimilated arsenic concentrations.²⁹

Total arsenic whole-tissue concentrations in *T. marioni* and *Arenicola marina* have been found to be independent of age/size and dry mass,^{13,23} indicating arsenic bioaccumulation is similar for juveniles and adults. However, insufficient data are available to support or refute that this occurs for all polychaetes.

Arsenic concentrations in polychaete tissues can vary greatly. Thorax tissue of the suspension-feeding polychaete *Sabella spallanzanii* had $48 \pm 19 \mu\text{g}$ arsenic/g dry mass,²⁸ whereas the branchial crown had $1036 \pm 136 \mu\text{g}$ arsenic/g dry mass (Table 2). Gibbs *et al.*²³ found that the polychaete *T. marioni* had extreme arsenic 'hyper-accumulation' characteristics. *T. marioni* have the highest concentrations of arsenic ever recorded in whole animal tissues, i.e. 2739 μg arsenic/g dry mass (Table 1). Arsenic is mostly concentrated in the palps (feeding appendages), which contain 6327 to 13 048 μg arsenic/g dry mass. This represents ~20% of the whole body arsenic bioaccumulation of *T. marioni*, even though these organs represent only ~4% of the body mass. The total arsenic concentration was remarkably consistent from individual to individual and was maintained irrespective of the ambient arsenic concentration. It is thought that arsenic in this animal has an essential cellular or metabolic function; however, another species of *Tharyx*, and two more from the Cirratulid family, collected from the same locations, did not bioaccumulate arsenic to similar concentrations, casting some doubt as to the essentiality of arsenic in *T. marioni*.

WATER-SOLUBLE ARSENIC SPECIES IN POLYCHAETE TISSUES

Most polychaete species examined to date (*Notomastus* spp., *Marphysa sanguinea*, *Nereis diversicolor* and *Nereis virens*) contain the majority of their arsenic as arsenobetaine (AB) (57–98%), with trace concentrations of inorganic arsenic species (<1%; Table 2, Figs 1 and 2). Thus, most arsenic species profiles in polychaete whole tissue are similar to the majority of marine animals analysed and reported in published literature.¹ It is unlikely that the polychaete species accumulated AB directly from interstitial water and/or sediments, as AB has been reported to be readily degraded to dimethylarsinic acid (DMA), trimethylarsine oxide (TMAO) and inorganic arsenic species under both anaerobic and aerobic conditions in marine sediments.^{31,32} AB is probably accumulated by infaunal polychaetes via organic food sources within the sediment. The presence of relatively high proportions of phosphate arsenoriboside (up to 12%) in some omnivorous polychaete species, i.e. Nereididae, may be due to ingestion of macroalgae, benthic diatoms and/or phytoplankton. Macroalgae contain arsenoribosides^{1,33} while herbivorous animals also contain arsenoribosides.^{34–36} The various *Nereis* species examined also have very similar

Table 1. Total arsenic concentration in polychaete whole tissues

Polychaete species	Location	Feeding guild ^a	Depuration (days)	Total [As] ($\mu\text{g g}^{-1}$) ^b	Sediment [As] ($\mu\text{g g}^{-1}$)	Ref.
Family Nereididae						
<i>Nereis diversicolor</i>	Bregner Bukt, Odense Fjord, Denmark	OROS and/or P	2	16 \pm 5	0.5 \pm 0.04	20
<i>Nereis diversicolor</i>	Southampton Town Quay, Great Britain	OROS and/or P	Physical exclusion of gut contents attempted	5	10 (Surface) 6 (10 cm depth)	21
<i>Nereis diversicolor</i>	Southwest England	OROS and/or P	7	6–87	(Surface) 7–2500	22
<i>Nereis diversicolor</i>	Rest of England and Wales	OROS and/or P	7	4–27	(Surface) 2–94	22
<i>Nereis diversicolor</i>	Northwest England	OROS and/or P	7	20 \pm 5	42 \pm 16	22
<i>Perinereis cultrifera</i>	Place Cove, Fal Estuary, south-west England	OROS and/or P	6	32	(Surface) 4	23
<i>Perinereis</i> spp.	Japan	OROS and/or P	Unstated	5	Unavailable	24
<i>Nereis succinea</i>	Mouth of Patuxent River, Chesapeake Bay, USA	OROS and/or P & DFO	Not undertaken	8	~7 \pm 4	10
<i>Nereis succinea</i>	Mouth of Patuxent River, Chesapeake Bay, USA	OROS and/or P & DFO	Not undertaken	5	2	11
<i>Nereis virens</i>	Netherlands	OROS and/or P	2	11 \pm 3	Unavailable	20
<i>Eunereis longissima</i>	Place Cove, Fal Estuary, southwest England	DFO	6	68	(Surface) 4	23
Family Eunicidae						
<i>Eunicidae</i> spp.	Waterman and Cockburn Sound, Western Australia	OROS and/or P	Not undertaken	23 (wet mass)	Unavailable	16
<i>Eunicidae</i> spp.	Chain Valley Bay, Lake Macquarie, NSW, Australia	OROS and/or P	Unstated	6	Unavailable	19
<i>Marphysa sanguinea</i>	Lake Macquarie, NSW, Australia	OROS and/or P	Unstated	72 \pm 31	12 \pm 2	25
Family Onuphidae						
<i>Onuphid</i> spp.	Gulf of Nicoya, Costa Rica, Central America	OROS and/or P	Not undertaken	32–107	8–14	26
Family Glyceridae						
<i>Glyceridae</i> spp.	Waterman and Cockburn Sound, Western Australia	OROS and/or P & DFO	Not undertaken	13 (wet mass)	Unavailable	16
<i>Glyceria convoluta</i>	Place Cove, Fal Estuary, southwest England	OROS and/or P	6	202	(Surface) 4	23

(continued overleaf)

Table 1. (Continued)

Polychaete species	Location	Feeding guild ^a	Depuration (days)	Total [As] ($\mu\text{g g}^{-1}$) ^b	Sediment [As] ($\mu\text{g g}^{-1}$)	Ref.
Family Nephthyidae <i>Nephtys hombergi</i>	Place Cove, Fal Estuary, southwest England	OROS and/or P	6	188	(Surface) 4	23
Family Aphroditidae <i>Aphroditidae</i> spp.	Waterman and Cockburn Sound, Western Australia	OROS and/or P	Not undertaken	7–13 (wet mass)	Unavailable	16
Family Capitellidae <i>Notomastus</i> spp.	Lake Macquarie, NSW, Australia	DFO	Unstated	1.5	12 \pm 2	25
Family Cirratulidae <i>Tharyx marioni</i>	Place Cove, Fal Estuary, southwest England	DFO	6	1512	(Surface) 4	23
<i>Tharyx marioni</i>	Five estuaries in southwest England	DFO	6	1228–2739	(Surface) 5–613	23
<i>Tharyx</i> sp.	River Exe, England	DFO	6	197	(Surface) 7	23
<i>Caulleriella caputesocis</i>	Place Cove, Fal Estuary, southwest England	DFO	6	95	(Surface) 4	23
<i>Cirriiformia tentaculata</i>	Place Cove, Fal Estuary, southwest England	DFO	6	84	(Surface) 4	23
Family Arenicolidae <i>Arenicola marina</i>	Bregør Bukt, Odense Fjord, Denmark	DFO	2	51 \pm 10	0.5 \pm 0.04	13
<i>Arenicola marina</i>	Province of Brabant, Netherlands	DFO	1	46	28	27
Family Ampharetidae <i>Melinna palmata</i>	Place Cove, Fal Estuary, southwest England	DFO	6	26	(Surface) 4	23
Family Spionidae <i>Spionidae</i> spp.	Waterman and Cockburn Sound, Western Australia	DFO	Not undertaken	19 (wet mass)	Unavailable	16

^a OROS and/or P: opportunistic raptorial omnivorous scavenger and/or predator; DFO: deposit-feeding omnivore.^b Dry mass unless otherwise stated.

Table 2. Water-soluble arsenic species (%) in polychaete tissues

Polychaete species and tissue	Total As ($\mu\text{g g}^{-1}$) ^a	AB	Glyce-rol As-ribose	TMAP	AC	TMAO	TETRA	As (III)	DMA	MA	Phosphate As-ribose	As (V)	Unknown As anion	Ref.
Whole tissue														
<i>Marphysa sanguinea</i>	72	98	—	—	0.2	0.4	1.2	—	—	—	—	<0.1	—	25
<i>Notomastus</i> sp.	1.5	88	—	—	4	—	—	—	3.4	4	—	0.4	—	25
<i>Arenicola marina</i>	51	4.5	0.3	0.7	0.4	—	1.2	57	1	—	2.8	23	10	13
<i>Nereis diversicolor</i>	16	64	1.9	3.4	1	0.4	20	—	—	—	10	—	—	20
<i>Nereis virens</i>	11	57	5.3	3.4	—	—	29	—	—	—	2.8	0.8	—	20
Tissue/organ														
<i>Nereis virens</i>														20
Muscle	7	79	<0.7	2.6	—	<0.7	13.2	—	—	<0.7	2.6	0.7	—	
Parapodia	11	63	11	4.3	—	<0.5	9.4	—	—	<0.5	10.5	0.5	—	
Oesophageal glands	4	62	12.7	3.1	—	<1.2	9.6	—	—	<1.2	9.4	1.2	—	
Palps	8	61	8.7	2.2	—	1.8	12.6	—	—	<0.7	12.2	0.7	—	
Intestine	8	48	4.3	3.2	—	0.6	37.1	—	—	<0.6	4.7	1.8	—	
<i>Sabella spallanzanii</i> ^b														28
Thorax	48	13	—	—	—	—	—	—	83	—	—	—	—	
Branchial crown	1036	5	—	—	4.8	—	4.3	—	87	—	—	—	—	

^a Dry mass.^b Suspension-feeding omnivore living in sand and mud substrates.

high proportions of tetramethylarsonium cation (TETRA; 20–29%), which is not found in sediments or marine algae but is present in a variety of marine animals.¹ Generally, most arsenic found in polychaetes is water soluble rather than lipid soluble (Table 2). A notable exception is *T. marioni*, in which ~65% of the arsenic was lipid soluble.

Geiszinger *et al.*¹³ reported that 57% and 23% of the water extractable arsenic present in *A. marina* was arsenite and arsenate respectively (Table 2; Fig. 1), with AB present as only a minor constituent (4.5%) and with a relatively high concentration of an unknown anionic arsenic species (10%). Similarly, Fattorini *et al.*²⁸ reported AB to be a minor component in *S. spallanzanii* tissues (5–13%; Fig. 2) and that the major species was DMA (83–87%). Organoarsenic compounds in marine organisms, such as AB, are thought to represent non-toxic end products in a scheme for detoxifying harmful inorganic and simple methylated arsenic species.^{1,37} In contrast, arsenite is considered to be the most toxic of the arsenic species found naturally in the environment.³⁸ The presence of arsenite as the major arsenic species in *A. marina* suggests that this polychaete may have a species-specific physiological resistance to arsenite, or metabolically processes it in an unknown manner. *A. marina* also had a relatively high concentration of an unidentified anionic arsenic species (10%). Sediment is the likely source of this arsenic species, since an unidentified arsenic species with matching chromatographic data was also detected in sediments forming the habitat for the

A. marina analysed. DMA is less toxic than arsenite/arsenate,¹ and high concentrations of DMA in *S. spallanzanii* may be a response to exposure to inorganic arsenic.

ARSENIC BIOACCUMULATION BY POLYCHAETES IN RESPONSE TO ENVIRONMENTAL EXPOSURE AND CONDITIONS

There is a paucity of data that allows any generalizations of arsenic accumulation by polychaetes in response to prevailing physiochemical conditions and arsenic concentrations and species in water, food and sediments. When we plotted published arsenic concentrations in sediments versus polychaete arsenic concentrations, no significant relationship was found (Fig. 3). *N. diversicolor* collected from 15 locations, with a surface sediment total arsenic concentration range of 0.5–2500 $\mu\text{g g}^{-1}$ dry mass, had a whole-tissue total arsenic concentration range of 4–87 $\mu\text{g g}^{-1}$ dry mass, demonstrating the non-linear accumulation of arsenic by this polychaete species with respect to sediment-bound arsenic. Geiszinger *et al.*^{13,20} demonstrated that *A. marina* and two *Nereis* species accumulated arsenate from seawater in the absence of sediment in a dose-dependent manner and that the *A. marina* enrichment/concentration factor was higher than that for either of the *Nereis* species. *A. marina* accumulated arsenic as

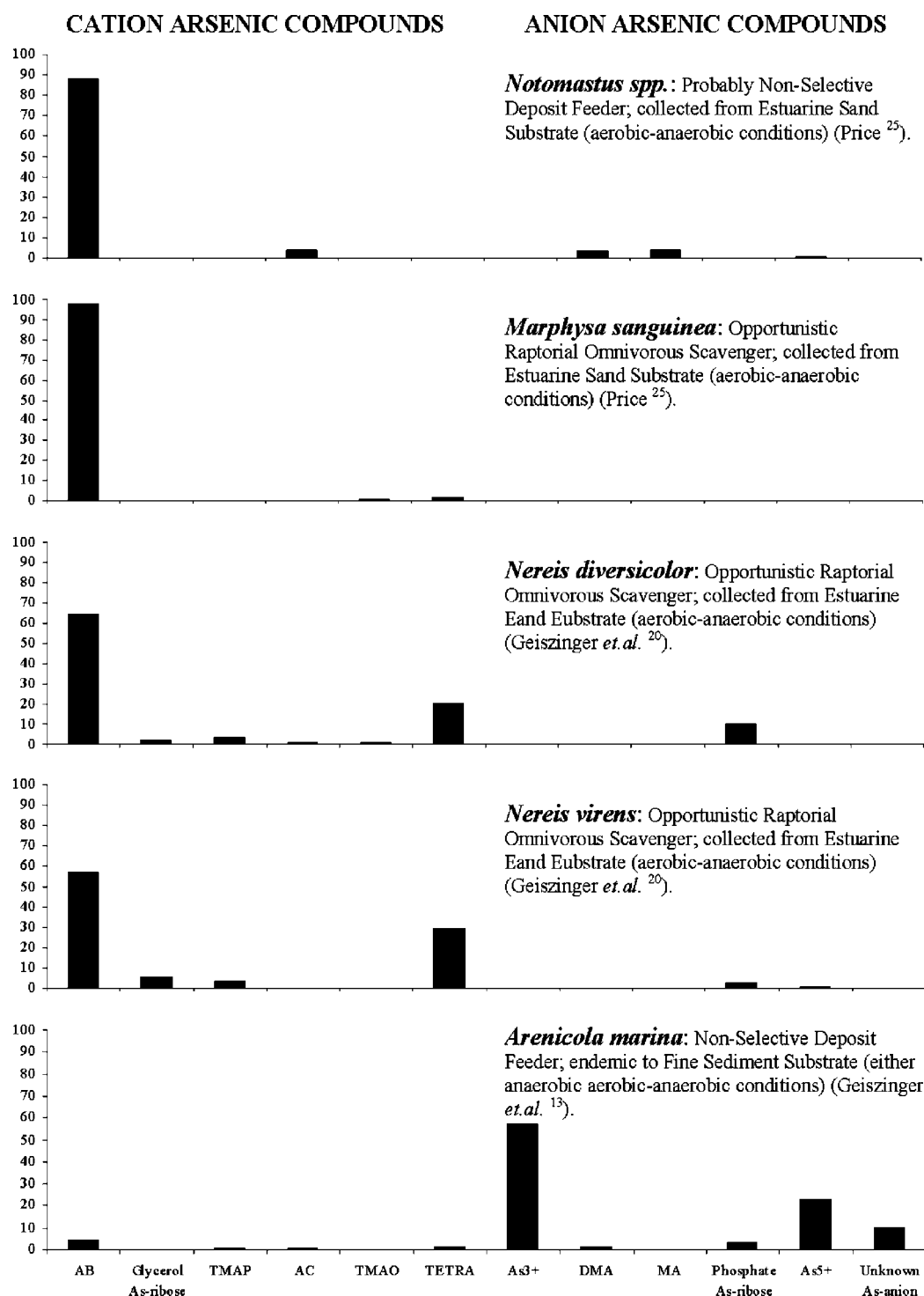


Figure 1. Water-soluble arsenic species proportions (%) in whole tissues of five infaunal polychaete species.

arsenate with small amounts of DMA (1–5.2%), and TETRA ($\leq 3\%$), whereas the Nerid species readily methylated arsenic to TETRA ($\sim 85\%$). However, these polychaetes were exposed to unrealistically high dissolved arsenic concentrations and under natural conditions probably do not accumulate arsenic via this route.

These results give rise to questions about the relative importance of ambient environmental conditions, species-specific physiology, trophic position and exposure to arsenic species through food or sediment intake as factors influencing arsenic bioaccumulation by polychaetes and the arsenic species proportions found.

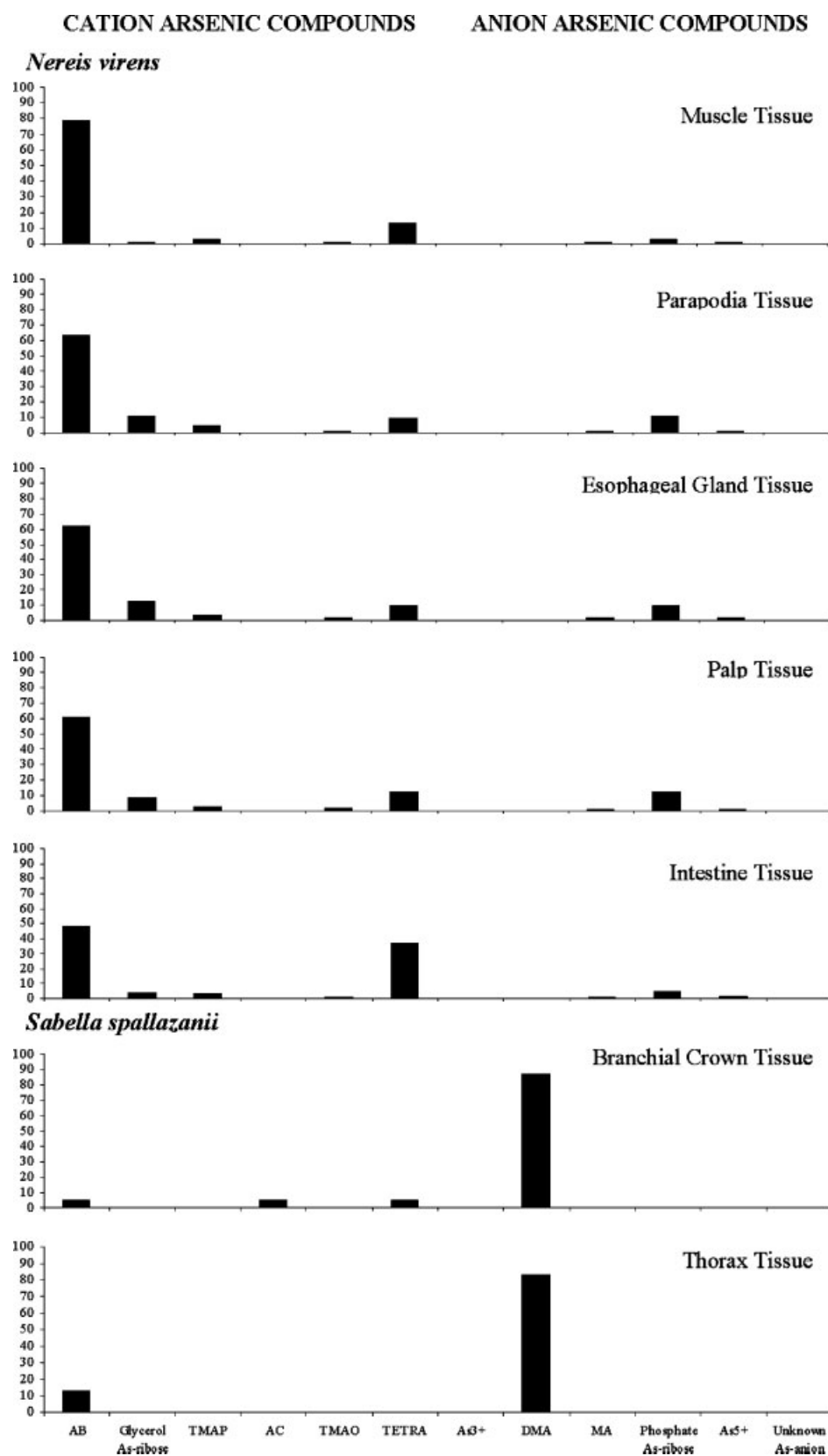


Figure 2. Water-soluble arsenic species proportions (%) in tissues of *Nereis virens* (Geiszenger *et al.*²⁰) and *Sabella spallanzanii* (Fattorini *et al.*²⁸).

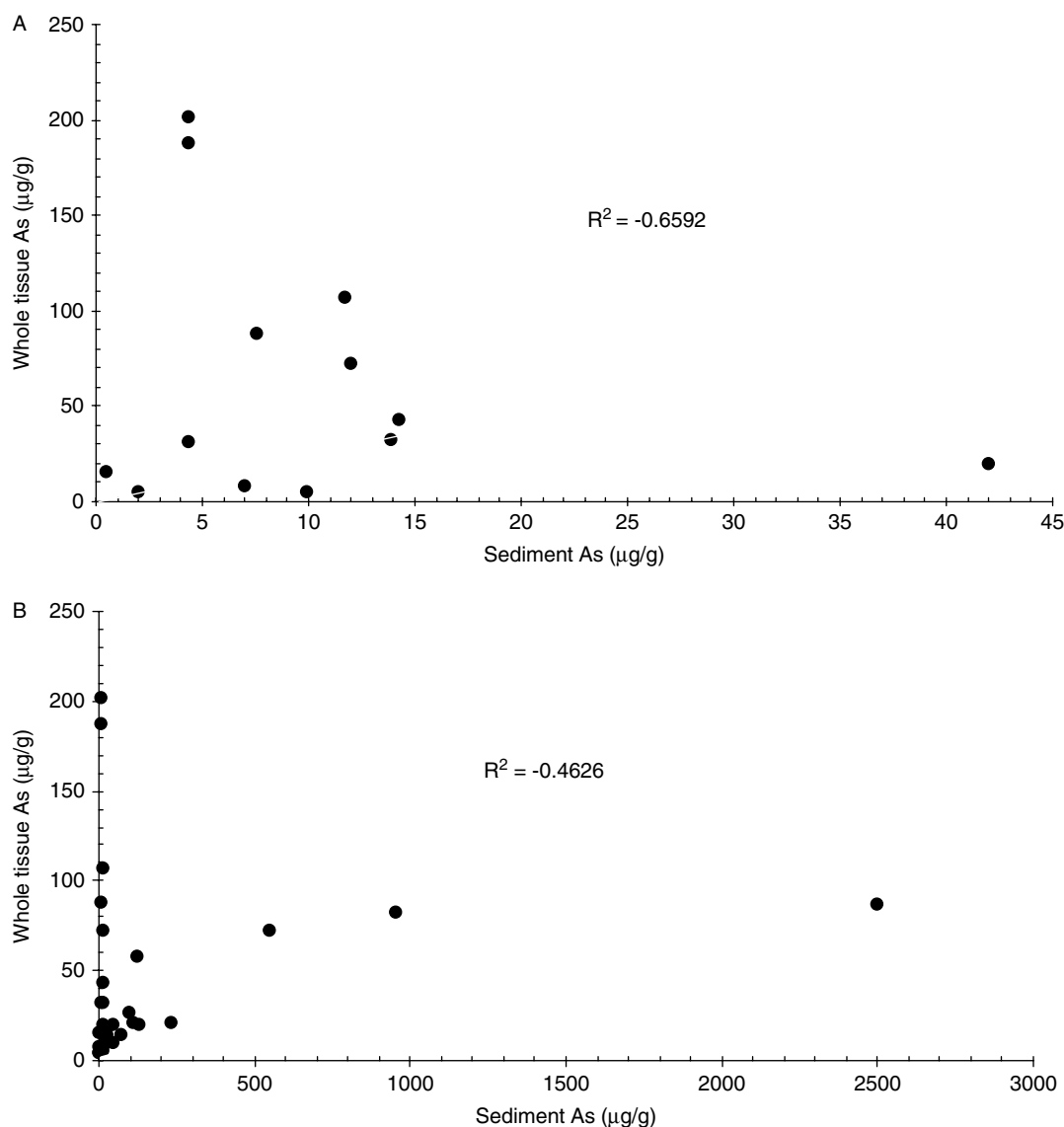


Figure 3. Relationship of arsenic concentrations in polychaetes and sediments: (A) low sediment arsenic concentrations; (B) all data.

EXTRINSIC AND INTRINSIC FACTORS INFLUENCING ARSENIC BIOACCUMULATION IN POLYCHAETES

Arsenic bioaccumulation in polychaetes is similar by analogy to trace element accumulation (Fig. 4) and will be controlled to varying degrees by combinations of intrinsic and extrinsic, biological, physical and chemical factors.^{39–42} Intrinsic factors include: polychaete osmoconformer physiology; species-specific uptake and regulation; genetic diversity; feeding preferences, digestive tract biochemistry (enzymatic hydrolysis, microbes and diet); physiological state (especially nutritional state and reproductive condition); and gender.^{39,41–43} Extrinsic factors include: physiochemical properties of arsenic species and ambient concentration; ambient pH, salinity, temperature dissolved oxygen concentration and

redox potential; co-presence and competition with other trace metals; ambient concentrations of sulfides and other chelating agents; food availability and sediment organic carbon content^{39–44} and temperature.

The relative importance of different bioaccumulation pathways will depend on the ecology of the polychaete species and the habitat-specific geochemistry of arsenic.^{40,41} Polychaetes will be exposed to arsenic in both the solute (sediment interstitial and overlying water) and particulate (sediment and food) phases (Fig. 4). Infaunal polychaetes may take up arsenic species from direct exposure to particulate-phase arsenic through ingesting sediment,^{11,23,41} dissolved-phase arsenic from interstitial water via adsorption through the epithelium and/or absorption through respiratory/digestive membranes,⁴¹ and by consuming organisms that bioaccumulate arsenic.¹⁹

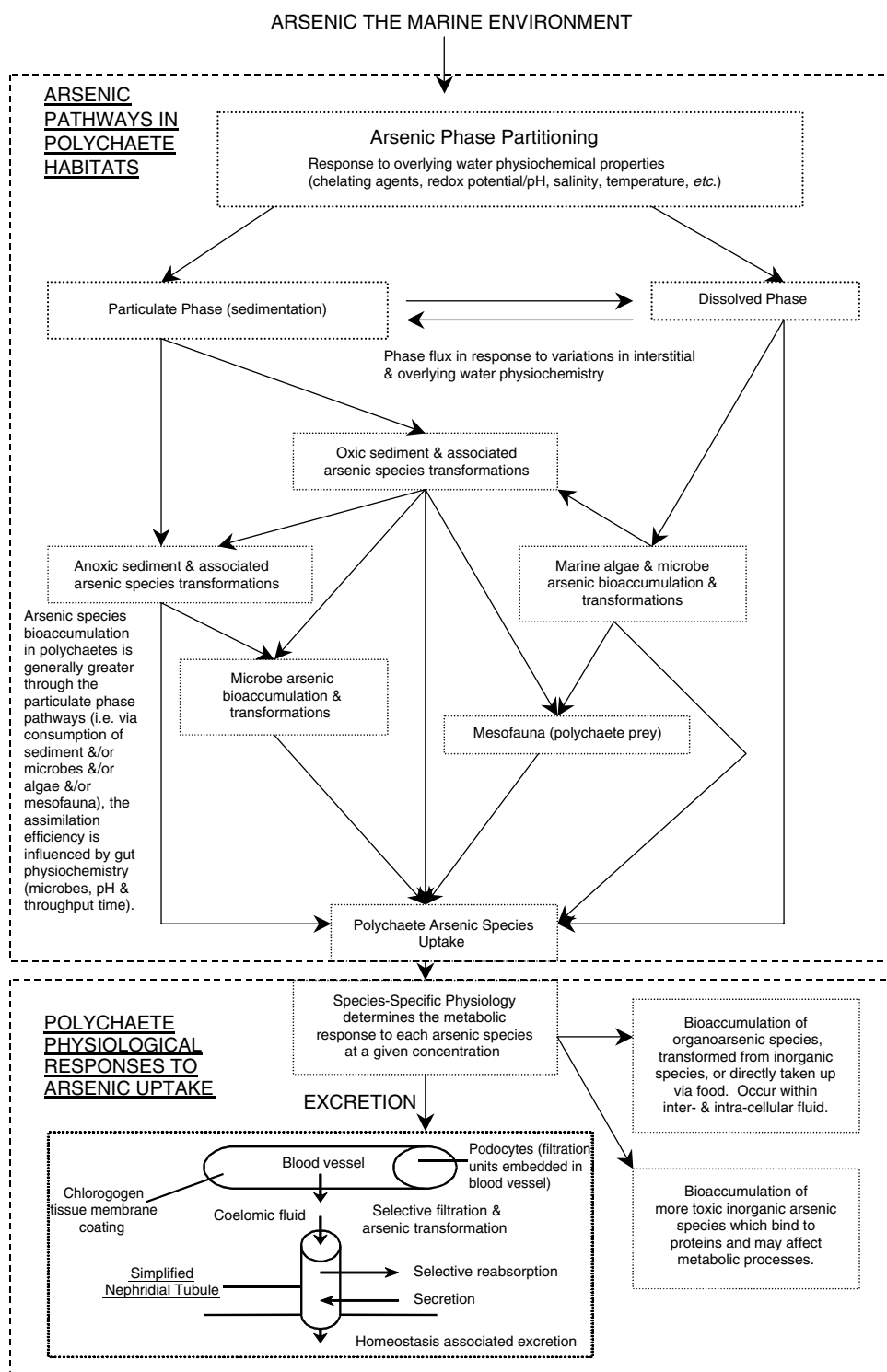


Figure 4. Polychaete arsenic bioaccumulation pathways.

ENVIRONMENTAL ARSENIC EXPOSURE: ARSENIC SPECIES

Arsenic has a complex biogeochemical cycle in marine ecosystems, involving biologically mediated and abiotic

redox chemistry controlled transformations^{10,11,37} (Fig. 5). In this cycle, concentrations of the most toxic arsenic species, arsenite, usually remain very low in all but anoxic micro-environments.^{37,44,45} The relative proportions of inorganic and organic arsenic species at any given time in marine

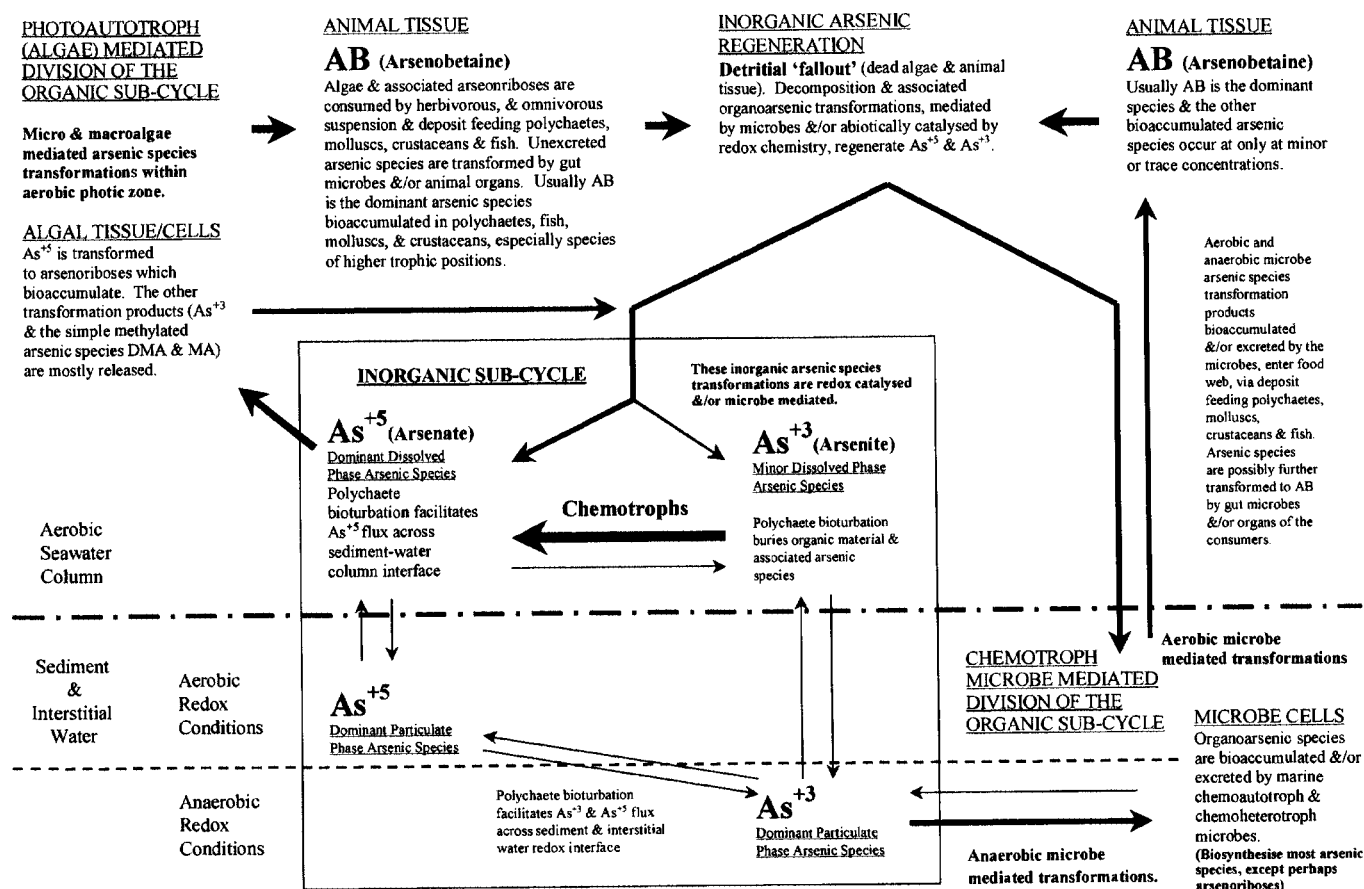


Figure 5. Marine arsenic cycle.

and estuarine waters and sediments depend on: the redox conditions; temperature and salinity; and algae and bacteria species and abundance.^{10,11,37,45,46}

The marine arsenic cycle appears to consist of two distinct sub-cycles: an inorganic arsenic species sub-cycle, controlled by redox chemistry and microbial-mediated oxidation and reduction,^{1,37,45} and an organoarsenic species sub-cycle,^{1,37} in which phytoplankton, macroalgae and bacteria produce and transform arsenic species^{33,45,47} (Fig. 5). Photoautotrophs and chemotrophs that convert inorganic arsenic species to organoarsenic species and facilitate the flux between the inorganic and organic species sub-cycles.

If arsenic is being obtained via adsorption from interstitial waters, then, depending on whether contact is with aerobic or anaerobic sediments, polychaetes will be exposed to different arsenic species (Fig. 5).

The photoautotrophs (algae), restricted to photic depths while alive, predominately contain arsenoriboses, arsenate, arsenite and simple methylated arsenic species.^{1,33,47} Arsenoriboses have been identified in a variety of marine animals,^{13,20,34} including three species of infaunal polychaetes.^{13,20} Thus, arsenic species in algae may be

consumed and directly taken up by suspension-feeding, herbivorous and surface-deposit-feeding polychaetes.

Chemoautotrophs that utilize inorganic and organoarsenic species (i.e. bacteria, yeasts, etc.) occur in both the water column and aerobic and anaerobic sediments.^{1,31,32,46,48} Chemotroph taxa have been found capable of bioaccumulating, biosynthesizing, and excreting most arsenic species found in the marine environment, except AB, arsenocholine (AC), trimethylarsoniopropionate (TMAP) and arsenoriboses.^{1,31,37,46,48,49} Organoarsenic compounds, including AB, once released into the marine environment are also degraded rapidly to arsenate by chemoautotrophs.^{31,32} Chemotrophic bacteria are thought to play a major role in detoxifying arsenic in the marine environment, mediating up to 90% of arsenite transformation to arsenate^{37,46,47,49} (Fig. 4). Chemotroph arsenic species may be directly bioaccumulated through consumption of sediment and/or exposure via sediment interstitial water by suspension and infaunal polychaetes, especially deposit feeders.

The most abundant arsenic species in marine animals is AB.^{1,20,25,35–37} Notable exceptions are the sea squirt *Halocynthia roretzi*,⁵⁰ the herbivorous teleost fish *Kyphosus sydneyanus* (silver drummer),⁵¹ the bivalve mollusc *Corbicula japonica*⁵¹

and the mammal *Dugon dugon*,⁵² all of which do not contain AB in some tissues. Marine animals can also contain other arsenic species, usually as minor constituents, including TMAO, TETRA, AC, phosphatidylarsenocholine, DMA, TMAP and one or more of the range of arsenic-containing carbohydrates known collectively as arsenoribosides or arsenosugars.^{1,34–36} Inorganic arsenic species (arsenate and arsenite) and simple methylated arsenic species (MA, DMA, TMAO, TETRA) are sometimes also present in marine animals, generally as trace constituents, although the polychaete *A. marina*,¹³ the polychaete *S. panllanzanii*²⁸ and the gastropod *Hemifusus ternatanus*³⁷ are notable exceptions. Many polychaetes are carnivores or scavengers and will consume AB and other minor arsenic species in their prey or the detritus they consume.

Infaunal polychaetes may themselves exert a substantial influence on the cycling of arsenic compounds in marine ecosystems.^{11,53} Infaunal polychaetes facilitate the movement of inorganic and organic arsenic species across the sediment–water column interface by burrowing and feeding (bioturbation), and through respiratory and excretory activities.^{10–12} Methylation of inorganic arsenic by or within polychaetes can also occur.^{13,20}

ENVIRONMENTAL ARSENIC EXPOSURE: HABITATS, FEEDING PATTERNS AND PHYSIOLOGY

Four distinct microhabitats based on foraging activity can be identified (Fig. 6); sessile epifauna suspension feeders, and infauna foraging activity that occurs in (1) predominately aerobic sediment, (2) a region spanning the sediment redox interface (aerobic–anaerobic conditions), and (3) predominately anaerobic sediment. The arsenic concentration and species composition in food items (including mesofauna prey, sediment organic carbon and associated microbes) will vary between these microhabitats as previously discussed.

Sessile epifaunal suspension-feeding polychaete species living in sand or mud are in close proximity to the sediment surface and ingest larger amounts of suspended sediment and associated food items (organic carbon, benthic diatoms, microbes and mesofauna) than polychaetes living on hard rock substrates high in the water column, which consume predominately phytoplankton and zooplankton. The association of dietary items with particular sediment types (gravel, sand, silt) may directly influence the amount of arsenic and arsenic species bioaccumulated.

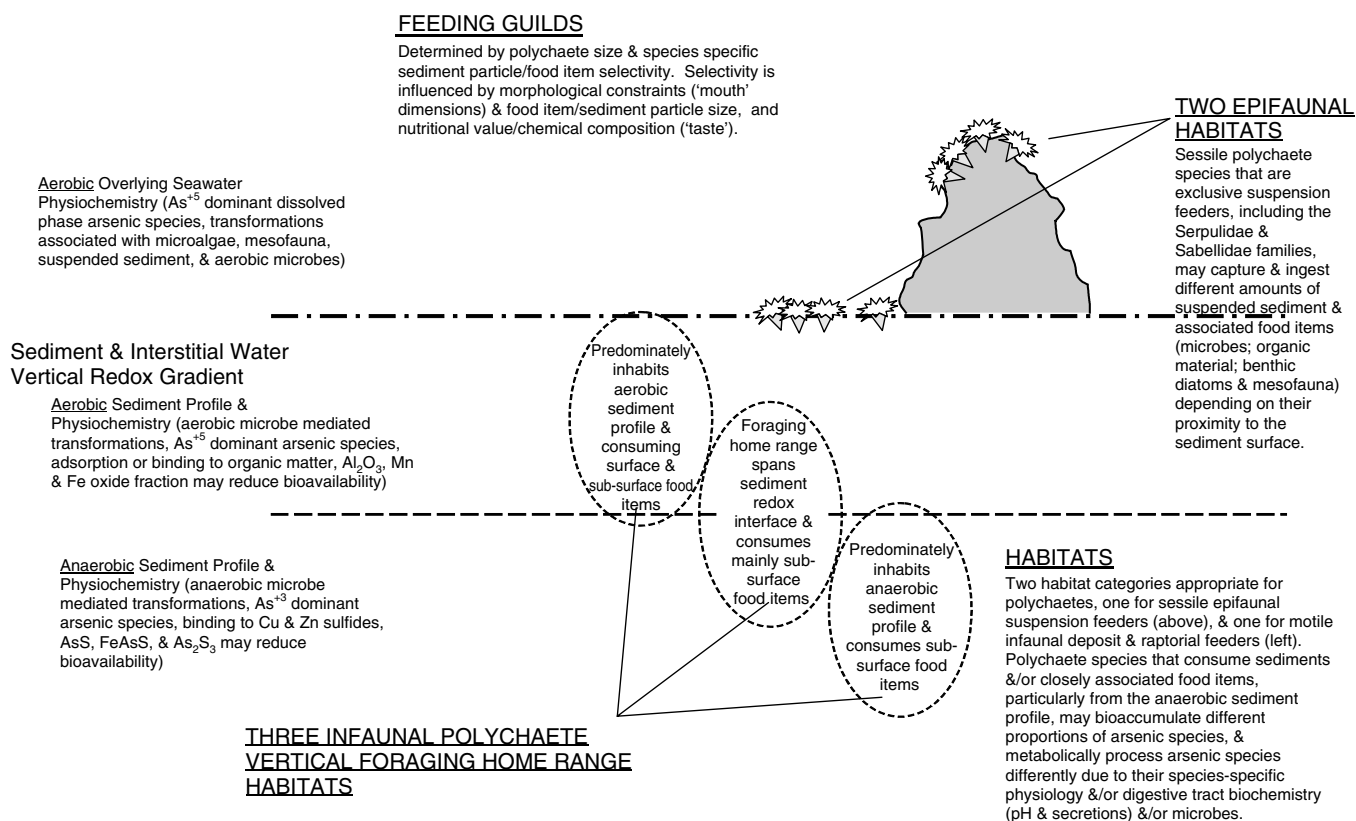


Figure 6. Foraging behaviour of polychaetes that may directly influence the bioavailability and bioaccumulation characteristics of arsenic.

The feeding strategies of polychaetes are closely correlated with the habitats they occupy.⁵⁴ Polychaetes can be highly mobile (errant), sedentary or sessile, but the distinction is not always sharp.⁵⁴ Feeding strategies include combinations of carnivory, herbivory and scavenging (collectively referred to as raptorial), suspension feeding, selective or non-selective deposit feeding; and in a few species even parasitism.^{2,4,5,54,55} Some infaunal polychaetes and all sessile polychaetes are suspension feeders, and may be considered omnivores, although to a large extent their diet often comprises microalgae, with the associated ingestion of suspended particulates covered in a microbial film and zooplankton.^{2,3,6,54,56} Raptorial feeding refers to a polychaete's use of its mouth to seize food items.^{2,5} Opportunistic omnivorous feeding behaviour occurs in most feeding guilds, and variations in feeding strategies can occur within a genus.^{2-7,20,54} Many polychaete species possessing jaws are probably highly opportunistic and can feed on a wide range of food,^{2,5,6,57} although the efficiency with which they can utilize food has not been studied for many species.² Certainly, faecal pellets often contain algal remains, suggesting a willingness to consume algal matter, but a limited ability to break it down due to digestive constraints, perhaps indicating a lack of the enzyme cellulase in digestive systems,² and/or fermentative gut microbes, appropriate gut architecture and throughput time allowing effective digestion.⁷

Deposit-feeding polychaete species swallow particulate organic matter, mud and/or sand, obtaining nutrients from their contents and/or the fine layer of algae and/or microbes coating each particle.^{3,6} Polychaetes select specific food items and/or sediment particles because of constraints such as mouth dimensions and food item nutritional value.^{2,6,7} The degree of dietary selectivity may influence arsenic bioaccumulation. For example, the relatively sedentary, selective deposit-feeding polychaete family Pectinariidae, by particle selection, concentrates organic matter from about 32% mass/mass (in sediment) to 42% mass/mass (in the gut). Of the ingested organic fraction, about 30% mass/mass is utilized and the remainder passes through the gut.⁵⁴

In summary, in uncontaminated environments, ingested material is probably the major arsenic uptake pathway for polychaetes.²³ Total arsenic concentration and arsenic species composition differences among polychaete species with similar feeding strategies (Tables 1 and 2) may be due to different food item selectivity and digestive capacities. Polychaete digestive capacity may also differ between species with the same food item preferences,⁷ which may account for differing arsenic bioaccumulations between polychaete species, and similarities among polychaete species with different ecologies.

Polychaete species lifestyle within a specific habitat defines its vertical foraging home range (Fig. 6) and physiochemical environment to which it is physiologically adapted. The sediment physiochemistry (redox potential, salinity, pH, dissolved oxygen concentration, etc.) influences the exposure to and bioavailability of dissolved and particulate-phase arsenic compounds. Infaunal polychaete species can inhabit

aerobic sediments, anaerobic sediments or both, and have adapted to these habitats. Therefore, differences in arsenic bioaccumulation by polychaetes occupying similar locations may be also associated with physiologies adapted to the different redox conditions, etc. of these microhabitats. This may explain the wide variation in polychaete total arsenic concentrations reported in published scientific literature and the lack of a similar range of arsenic concentrations in other marine animals groups examined.^{1,58} When examining arsenic bioaccumulation at specific locations, microhabitats characterized by different physiochemical characteristics need to be considered.

The influence of polychaete microhabitat, feeding strategies and physiology on arsenic bioaccumulation is supported by all the field studies reviewed, in which mean whole-tissue total arsenic concentrations in different polychaete taxa, collected from the same locations, are different.^{16,20,23,25} Total arsenic concentration variability even within Polychaeta taxon can also be seen from results available for the polychaete family Cirratulidae, where three of its species (*T. marioni*, *Caulleriella caputesocis*, and *Cirriformia tentaculata*), which are errant, selective, surface-feeding, jawless, deposit-feeding omnivores^{3,6} and collected from the same location, contained mean whole-tissue total arsenic concentrations of 1512 µg, 95 µg, and 84 µg arsenic/g dry mass respectively²³ (Table 1). Thus, interpretation of arsenic data will require a clear understanding of polychaete ecology, particularly its microhabitat type, feeding strategies and physiology, to explain the different arsenic bioaccumulation characteristics of polychaete species.

Geiszinger *et al.*²⁰ suggest that polychaete physiology may be the most important factor determining whole-tissue total arsenic concentration and arsenic species proportions, not the arsenic species in food consumed or ambient redox conditions. Two related polychaete species from uncontaminated environments, *N. diversicolor* and *N. virens*, have similar proportions of arsenic species (Table 2, Fig. 1). They are both members of the same genus and are both errant, surface- and subsurface-feeding, jawed, predatory opportunistic omnivores, yet *N. diversicolor* was collected from Bregner Bugt and *N. virens* was reared in a distant Dutch bait farm. All factors considered, their diets and environments would be expected to be very different and, therefore, their exposure to ingested and ambient arsenic concentrations and arsenic species would also be very different. Geiszinger *et al.*²⁰ suggests that the taxonomic similarity of *N. virens* and *N. diversicolor*, and presumably physiological similarities, is the most influential factor determining arsenic accumulation and species proportions in polychaetes.

SUMMARY AND CONCLUSIONS

Polychaete species are physiologically adapted to specific habitats and have different feeding strategies. Thus, the large differences in total arsenic concentrations of polychaetes

reported in the published scientific literature may be due to habitat and feeding differences which control exposure to arsenic species and arsenic bioavailability as well as physiological adaptation to ecological niches that probably controls bioaccumulation. Most polychaete species analysed to date contain AB, but this is not always the case, with unusually high proportions of arsenite (58%), arsenate (23%) and DMA (83–87%) in some polychaete species. Consideration of the ecology of individual polychaete species in terms of their habitat type, feeding strategies and physiology is needed for the assessment of the potential arsenic uptake pathways and the polychaete species-specific bioaccumulation of arsenic. Future research should collect a range of polychaete species from a wide variety of uncontaminated marine habitats to determine the influence of these ecological factors on total arsenic concentrations and species proportions.

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