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Review

Bottom-up and top-down triggers of diversification: A new look at the evolutionary ecology of scavenging amphipods in the deep sea

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ABSTRACT

The initial, anthropocentric view of the deep ocean was that of a hostile environment inhabited by organisms rendered lethargic by constant high pressure, low temperature and sparse food supply, hence evolving slowly. This conceptual framework of a spatially and temporally homogeneous, connected, strongly bottom-up controlled habitat implied a strong constraint on, or poor incentive for, speciation. Hence, the discovery in the late 1960s of high species diversity of abyssal benthic invertebrates came as a surprise. Since then, the slow-motion view of deep-sea ecology and evolution has speeded up and diversified in the light of increasing evidence accumulating from *in situ* visual observations complemented by molecular and other tools. The emerging picture is that of a much livelier, highly diversified and more complex deep-sea fauna than previously assumed. In this review we examine the consequences of the incoming information for developing a broader view of evolutionary ecology in the deep sea, and for scavenging amphipods in particular. We revisit the food supply to the deep-sea floor and hypothesize that the dead bodies of animals, ranging from zooplankton to large fish are likely to be a more important source of food than their friable faeces. Camera observations of baited traps indicate that amphipod carrion-feeders arrive within hours at the bait which continues to draw new individuals for days to months later, presumably by scent trails in tidal currents. We explore the different stages of food acquisition upon which natural selection may have acted, from detection to ingestion, and discuss the possibility of a broader range of food acquisition strategies, including predation and specializations. Although currently neglected in deep-sea ecology, top-down factors are likely to play a more important role in the evolution of deep-sea organisms. Predation on amphipods at baits by bathyal and abyssal fishes, and large predatory crustaceans in the hadal zone, is often observed. Finally, we develop hypotheses regarding the effects of past, present and imminent anthropogenic activities on scavenger biomass and how these can be tested with the most modern tools.

1. Introduction: deep-sea dynamics

Over the course of the last two centuries the human's eye view of the deep ocean has undergone radical changes. In the beginning of the 19th century it was thought that increasing pressure with depth would compress water to such an extent as to prohibit life and even arrest sinking objects (including ships and cargoes) in mid-depths where water density was believed to equal that of lead or iron (Denny, 2008). Although this notion was strongly disproved in the second half of that century, both by evidence of diverse life forms at the sea floor and by experimental demonstration that water is practically non-compressible, pressure as a fundamental and universal problem for all organisms continues to linger in the collective mind-set. This was reflected in further views on life in the deep-sea habitat: a sparse food supply consisting of a slow rain of sinking particles – the waste products of the surface and intervening layers – fuelling a slow metabolism. But then deep-sea organisms were not in a hurry since it was constantly cold and there were neither diel nor seasonal rhythms to mark the passage of time. The discovery of the living fossil mussel – *Neopilina* (e.g. Clarke and Menzies, 1959) – in the deep sea further cemented the idea that even the rate of evolution – speciation – was slowed down by the pressure of constancy. This was the view prevalent until the 1960s and 1970s, when the extraordinary diversity of deep-sea life was finally appreciated with the general use of fine-meshed dredges and sieves (Gage and Tyler, 1991).

Dynamics was introduced into the dull view of deep-sea evolutionary ecology by the bomb tests of the 1950–60s whose fallout indicated that substantial vertical transfer of organic particles from the

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surface to the deep-sea floor must have occurred in surprisingly short time scales. Zooplankton faecal pellets were strongly suspected to be the vehicles. The first sediment traps deployed in the deep sea were located in the North Atlantic where they captured the anomalous feature of this oceanic region – the spring phytoplankton bloom – as a strong seasonal signal to depths below 3000 m (Deuser et al., 1981). Rapid sinking to depth of the spring diatom bloom was confirmed by time lapse cameras, also in the North Atlantic, that recorded the arrival of a layer of fluff on the sea floor at 4000 m within weeks of the surface peak (Lampitt, 1985). Since then diatomaceous fluff has been recorded on the deep-sea floor from many regions underlying high surface productivity (Beaulieu, 2003).

Interestingly, the role of dead animals settling out on the deep-sea floor, ranging from copepods to whales, was initially given little thought although some reflection would have suggested that they must have at least as much importance as the faeces. Indeed, Agassiz (1888) already considered dead bodies of large pelagic animals as an important deep-sea food supply, followed by phytoplankton and faeces (Stockton and DeLaca, 1982). The unfolding big picture of life in the deep sea, brought to our eyes by the cameras of increasing numbers of baited traps and deep-sea vehicles, is revealing a much greater degree of complexity and breadth of variation than assumed so far. This new and largely unexpected knowledge now needs to be organised in a conceptual framework closer in its dynamics of organism interactions to those of the more familiar coastal and terrestrial realms than to previous scenarios of dull deep-sea evolutionary ecology. In contrast to ecosystems that tap external energy sources (light, chemical energy), organisms of deep-sea ecosystems (with the exception of hydrothermal vents and cold seeps) have no influence on enhancing their food supply by evolving symbiotic interactions between photo- or chemoautotrophic organisms and heterotrophs, i.e. recycling pathways cannot arise (McClain and Schlacher, 2015). Thus, deep-sea ecosystem biomass and structure is entirely dependent on the supply of external food and should serve as a robust indicator of its magnitude. If adequately estimated at relevant scales, the benthic biome should provide a more accurate proxy for vertical carbon flux than current methodology (sediment traps, sediment oxygen uptake) that sample at the m^2-scale. Region-scale assessments of the density and composition of the mobile scavenging fauna could improve estimates of the supply of organic carbon to the deep sea – a key component of the global carbon cycle that is presently not well constrained (Ducklow et al., 2001; Heinze et al., 2015).

2. The amphipod scavenger fauna

Amphipods, in particular those of the superfamily Lysianassoidea, are by far the most ubiquitous marine scavengers, thriving both in shallow-water and deep-sea ecosystems throughout the World's Oceans (e.g. Slattery and Oliver, 1986; De Broyer et al., 2004). In the hadal zone, where other scavengers such as decapods are less common, amphipods represent the major scavenging taxon (Blankenship and Levin, 2007). The Antarctic slope is known to harbour a particularly diverse and abundant amphipod scavenger assemblage (De Broyer et al., 2004), and some of these species have even been found under an ice shelf more than 400 m thick (the Ross Ice Shelf, Stockton, 1982). Many species are characterized by a benthopelagic lifestyle and hence they may also be important vectors for upward transfer of material from the sea floor (Smith et al., 1979).

The first scientific observations of the scavenging amphipod fauna were made using baited nets and traps as early as the late 19th and early 20th century. In the deep sea, bathyal and abyssal trap sampling was initiated by the Prince of Monaco on the *Hirondelle* in 1888 (Richard, 1934) whilst the early Antarctic explorers had already described the voracious feeding of amphipods on fish in baited nets (Walker, 1907). During their expedition in the Canadian Arctic (1881–1884), the shipwrecked crew of the Lady Franklin Bay Expedition even tried to overcome starvation by deploying baited traps (Greely, 1886). Much later, in the late 1960s, the development and use of specialized baited traps and time-lapse cameras literally shed light on a previously unsuspected but diverse deep-sea scavenger community (e.g. Isaacs, 1969; Hessler et al., 1972). Baited free-vehicles, equipped with cameras and devices programmed to release the weight used to sink to the seafloor, showed the presence of significant populations of small and large scavengers at abyssal depths under extremely oligotrophic waters (Sessions at al., 1968; Hessler et al., 1972). Hessler et al. (1972) reported the presence of a giant amphipod at bait deployed on the seafloor in the North Pacific and ever since, the prominent *Eurythenes gryllus* has been the principal focus of ecological and physiological studies on deep-sea organisms (Takeuchi and Watanabe, 1998).

2.1. Scavengers: definitions and roles in the food web

The last decade has been referred to as the golden age of scavenger research and a growing literature supports the evidence for the essential role of carrion and scavengers in ecology (Moleón and Sánchez-Zapata 2015), however this perspective is biased towards terrestrial research and does not hold true for the deep sea. Indeed, several questions raised more than three decades ago by Stockton and DeLaca (1982) remain unanswered so far, e.g. regarding the nature and frequencies of food falls, as well as the population sizes, turn-over rates and biogeography of motile scavengers such as amphipods. In the absence of direct observations of the natural feeding habits of the animals, information gathered from baited trap systems has strongly influenced the concepts applied to motile deep-sea fauna. As a first step, a consensus needs to be set since many different definitions have been used non-consistently in the scientific literature. In a comprehensive review Britton and Morton (1994) defined a scavenger as an organism 'able to detect carrion, usually by either distance or touch, chemoreception or both, deliberately move towards it, and eventually consume either part or all of it'. This definition is based on "carrion", defined by Wilson and Wolkovitch (2011) as a high-quality form of detritus that is composed entirely of dead animal matter and is clearly biased by the nature of the bait offered. It is often used in a much narrower sense than the accepted terrestrial definition of scavenger food which includes all dead organisms of both plant or animal origin (Getz, 2011). On the contrary, other authors also define in a more narrow sense both terrestrial and marine scavengers to be carcasivores (Moleón and Sánchez-Zapata, 2015), i.e. organisms that consume carrion, hence decaying flesh in the shape of carcasses. Throughout this review we will consistently use the term scavenger in its broadest sense, i.e. feeding on all dead organisms regardless of their origin, whilst when using the term carrion-feeder, we refer to feeding on animal carcasses larger than a centimetre. The term food fall is equally commonly used in deep-sea literature and this term stood alternately for large parcels of food such as carcasses of fishes, squids and marine mammals (e.g. Stockton and DeLaca, 1982), as well as for organic matter in a broader sense also including plant material such as macrophytes (e.g. Lawson et al., 1993), and we have opted to use the latter here. Since there is an extreme variation in detrital quality (Wilson and Wolkovitch, 2011), we distinguish between detritivores and scavengers with the former referring to organisms only feeding on small fragments of decaying organic matter.

Scavenging has been found to be largely underestimated in food web models because the use of carrion by vertebrates through facultative scavenging is much more widespread than implied by conventional theory (Wilson and Wolkovich, 2011). Whilst only some terrestrial animals are obligate carrion-feeders such as vultures and the larvae of carrion flies and burying beetles, nearly all vertebrate predators feed facultatively on carrion combining it with predation (e.g. bears, hyenas) or omnivory (pigs, crows) (DeVault et al., 2003). Recent ecological studies in the deep sea have shown that many presumed obligate scavengers are also predators. Thus, hagfishes (Myxinidae), commonly caught in baited traps, were thought to be scavengers in the deep sea, however video observations show that they were actively preying on sharks and bony fishes (Zintzen et al., 2011). Further, the Greenland sleeper shark (*Somniosus microcephalus*) often observed voraciously feeding on food falls and hence considered a true scavenger, only recently has been shown to be an apex predator on several rapidly-swimming fish species, as well as seals and sea lions (Nielsen et al., 2014).

Amphipods found in baited traps are currently classified as facultative, obligate or specialist carrion feeders. They have been extensively studied with regard to morphological adaptations for facultative and obligate carrion-feeding. These consist of modifications of the mouthpart bundle, suitable for slicing and chewing of larger food items such as widening and sharpening of the cutting edge of the incisor, modification of the molar process from the oval surface (*Orchomenopsis*-type) to the semi-tubular or flap-like molar found in species of the genera *Hirondellea* and *Eurythenes*, and the transformation of flat mandibles (*Orchomenopsis*) to strongly bowl-shaped ones (*Eurythenes*), allowing large portions of food to be scooped into the oesophagus (Dahl, 1979; De Broyer et al., 2004; Corrigan et al., 2014). Another adaptation considered important for the carrion-feeding mode is the enhancement of the storage capacity of the distendable foregut (in *Abyssorchomene*) or the midgut (in *Eurythenes*, *Paralicella*). However, the distinction between facultative and presumed obligate carrion-feeding based on the aforementioned mouthpart characteristics has by no means been straightforward as comparisons with ecological studies (e.g. gut contents analyses or feeding experiments, see Table 1) have shown (De Broyer et al., 2004). Divisions of labour and food partitioning at carcasses, reflected in mouth part morphology and behaviour, prevail among carrion-feeders in general, and amphipods in particular, as a result of adaptive speciation. Amphipods of the genera *Paracalissoma*, *Paralicella* and *Eurythenes* are the main consumers of a carcass, arriving first, whilst *Orchomenella*, *Abyssorchomene* species arrive later, hypothesized to be more generalist carrion-feeders that take advantage of the incisions in the skin the former species or ‘rippers’ have generated to enter the carcasses and feed upon the muscle tissue (e.g. Jones et al., 1998).

2.2. Phylogenetic histories and phylogeographic patterns of amphipod scavengers

Our knowledge on amphipod evolution is generally limited due to their poor fossil record. The few specimens found in Baltic amber resemble most closely the present-day subterranean and freshwater gammaridean genera and are dated to the late Eocene (35–40 Mya, e.g. Coleman, 2004, 2006). However, it is speculated that the origin of amphipods is much older, which is the case for other peracarid orders (isopods, mysids) (e.g. Fišer et al., 2013). Recent studies based on molecular tools have attempted to elucidate the evolutionary histories of shallow-water and deep-sea lysianassoid amphipods (Havermans et al., 2010, Corrigan et al., 2014, Ritchie et al., 2015) hence it is worthwhile to take stock of these findings. At the genus and family levels, the classification of lysianassoids is often based on morphological characters that are interpreted as adaptations to a more specialized necrophagous feeding mode. Havermans et al. (2010) showed for Southern Ocean lysianassoids that their monophyly was not supported at both these levels implying that these characters arose several times independently in the course of evolutionary history. When looking at deeper nodes in the phylogeny of the Lysianassoidea, species belonging to certain families also evolved morphological adaptations to carrion feeding several times independently in their evolution (Corrigan et al., 2014). An analogy comes to mind with vultures as scavengers of terrestrial systems that evolved separately in the old and new worlds but along convergent lines to very similar shapes and behaviour (Campbell, 2015). Based on a molecular phylogeny, Hou et al. (2011), estimated the origin of the genus *Gammarus* to approximately 61 Mya, and using this together with the gammaridean genera from the fossils dated at 35–40 Mya, as reference points, Corrigan et al. (2014) subsequently analysed the molecular phylogeny of North Atlantic lysianassoids and estimated their colonization of the deep sea by a shallow-water ancestor, around 70 Mya, coinciding with the Cretaceous-Palaeogene boundary. This molecular dating indicated that several scavenging amphipod families diversified rapidly from the Eocene-Oligocene boundary onwards (Corrigan et al., 2014). This rapid diversification of presumed obligate and specialist scavenger lineages, corresponding to genera such as *Eurythenes*, *Cyclocaris*, *Paralicella*, *Abyssorchomene* and *Stephonyx*, is congruent with the cooling and oxygenation of the deep ocean and was hypothesized to be triggered by an increased cetacean diversity and abundance, opening up a new ecological niche (Corrigan et al., 2014). However, it is well established that megafauna – from cephalopods to vertebrates – have inhabited the ocean for several hundreds of million years: for a cm-sized carrion-feeder it matters little whether the food fall is a 100 tonne whale or a kilogramme-sized nekton. In other words, cetaceans will have contributed only a small fraction of the carrion reaching the deep sea floor, and are in our opinion, if at all, not the sole triggers for this diversification.

Recent studies based on molecular tools have challenged previous concepts and paradigms regarding biogeography and species boundaries in the deep sea. The early view was that of a cosmopolitan and impoverished fauna inhabiting a spatially and temporally homogeneous, connected, strongly bottom-up controlled habitat which implied a strong constraint on, or poor incentive for, speciation. Hypotheses on a reduced species diversity and genetic differentiation in the abyss compared with shallower depths (the depth differentiation hypothesis, Etter et al., 2005) prevailed until recently but do not apply to several faunal groups, amongst others the carrion-feeding amphipods, which have undergone several diversification events in the abyss (Corrigan et al., 2014). The emblematic species *Eurythenes gryllus*, believed to be cosmopolitan, actually represents at least fourteen species that are both morphologically and genetically distinct (Havermans et al., 2013; Ritchie et al., 2015; Eustace et al., 2016; Havermans, 2016). Several species show overlapping distributions; most species are widespread, one has so far only been found under (sub-)polar waters, and some only in a particular trench or on a certain seamount. The commonly used arguments for the high diversity of deep-sea fauna and in particular scavengers are in our view not sufficient to explain the patterns observed. The belief that the upper bathyal zone (< 3000 m) is more prone to allopatric speciation, due to the topographic complexity (e.g. canyons) combined with a sediment heterogeneity and a more complex hydrography generated by these aforementioned topographic features does not seem to hold for scavenging amphipods: they are characterized by an equally high diversity in the abyss (Havermans, 2016). Scavenging amphipods can disperse easily and other gradients such as turbidity are too small-scaled to potentially influence their distribution. Several species of *Eurythenes* have distributions encompassing ridges and rises; hence, topographic features do not seem to be absolute barriers to dispersal – at least on evolutionary time scales – and do not, alone, promote speciation events. The same is true for *Paralicella* amphipods, for which a certain degree of gene flow and connectivity was revealed between populations inhabiting hadal trenches in the North and South Pacific, over large geographic distances (Ritchie et al., 2017). Further, invoking topographical as well as hydrographical barriers in the deep-sea environment to promote allopatric speciation implies that the organisms in question can sense large-scale spatial features and maintain themselves within it. We find this doubtful from the amphipod’s point of view, especially since deep water masses have, if at all, only very minor differences in temperature and salinity.

As an alternative, we provide an overview of potential features that could have driven speciation and diversification of amphipod scavengers in the deep ocean, developing a conceptual framework balancing bottom-up factors with top-down factors. Both competition and predation effects have long been allocated a negligible role in

Table 1
An overview illustrating the complexity of feeding habits of some amphipod scavengers. Data on amphipod diet based on molecular and morphological stomach content analyses, biomarker analyses, *in-situ* observations and feeding experiments are presented for amphipod species assumed to be obligate or facultative carrion-feeders, determined on morphological characteristics and their presence in baited traps. For several species, a regional variation in feeding habits exist. Question marks behind the predator feeding mode illustrate the fact that (pelagic) predatory habits are hypothesized but it cannot be excluded that the amphipods have been feeding on carcasses of pelagic animals on the deep-sea floor.

Species	Dietary items and traces	Methods	Morphology	Actual feeding habits	Reference
Abyssal – hadal					
Eurythenes gryllus – hadal populations in Pacific trenches	Tunicates, microeukaryotes, sediment grains, carrion, other lysianassoids	DNA, stable isotopes	Obligate carrion-feeder	Detritivore, predator?, carrion-feeder	Blankenship and Levin (2007)
Eurythenes gryllus – NE Atlantic, > 4800 m	Carrion	Lipid composition and fatty acids		Carrion-feeder	Bühring and Christiansen (2001)
Eurythenes gryllus – South Atlantic abyss	Sediment	Morphology (stomach content)		Detritivore	Barnard (1962)
Bathycallisoma schellenbergi – hadal populations in Pacific trenches	Tunicates, microeukaryotes (e.g. diatoms), sediment grains	DNA, stable isotopes		Detritivore, predator?, carrion-feeder	Blankenship and Levin (2007)
Hirondellea dubia – hadal populations in Pacific trenches	Diatoms, fungi, ciliates, other lysianassoids, fish (carrion)	DNA, stable isotopes		Detritivore, carrion-feeder, predator?	Blankenship and Levin (2007)
Hirondellea gigas – Philippine Trench, Pacific, 9600 m	Bacteria, sediment, diatom and radiolarian tests, nematodes and crustaceans	Morphology (stomach content)		Carrion-feeder, detritivore/benthic feeder	Hessler et al. (1978)
Paralicella caperesca – juveniles, North Atlantic	Sediment	Morphology (stomach content)		Detritivore	Smith and Baldwin (1982)
Abyssorchomene chevreuxi – Atlantic abyssal	Sediment (silt particles)	Morphology (stomach content)	Facultative carrion-feeder with adaptations for necrophagy	Detritivore	Chevreux (1903)
Tmetonyx cicada – NE Atlantic, 3000 m	Phytodetritus, crustaceans	Fatty acids and stable isotopes, phytodetrital bait deployments	Facultative carrion-feeder	Carrion-feeder, detritivore, predator?	Jeffreys et al. (2011)
Shelf – bathyal					
Eurythenes gryllus – Baffin Bay, N Atlantic	Fish	*In-situ* observations	Obligate carrion-feeder	Predator	Templeman (1967)
Hirondellea antarctica – Weddell Sea, Southern Ocean	Sponge spicules, hydrozoan remains, fish	Morphology (stomach content)		Micropredator on hydrozoans, carrion-feeder	Dauby et al. (2001)
Scopelocheirus sp. – Bahamas, 500 m	Macrophytes (*Sargassum*, *Thalassia*)	Trap deployment	Facultative carrion-feeder	Herbivorous feeding	Lawson et al. (1993)
Anonyx spp. (incl. *A. nugax*) – Atlantic, coastal	Pelagic polychaetes, crustaceans	Morphology (stomach contents)		Carrion-feeder, predator?	Sainte-Marie and Lamarche (1985)
Anonyx nugax – Barents Sea, shelf	Herbivorous copepods	Fatty acids		Carrion-feeder, predator?	Graeve et al. (1997)
Anonyx spp. juveniles – Atlantic, coastal	Detritus	Morphology (stomach contents)		Carrion-feeder, detritivore	Sainte-Marie and Lamarche (1985)
Anonyx compactus – Atlantic, coastal	Detritus	Morphology (stomach contents)		Carrion-feeder, detritivore	Sainte-Marie and Lamarche (1985)

(*continued on next page*)

Table 1 (*continued*)

Species	Dietary items and traces	Methods	Morphology	Actual feeding habits	Reference
Pseudorchomene plebs – Weddell Sea, Southern Ocean	Carrion, diatoms, crustaceans	Morphology (stomach contents)	Facultative carrion-feeder with adaptations for necrophagy	Carrion-feeder, detritivore, predator?	Dauby et al. (2001)
Pseudorchomene plebs – Gerlache Strait, Southern Ocean	Planktonic crustacean remains (copepods, euphausiids), fish, salps and “jellies”	Morphology (stomach contents)		Carrion-feeder, predator/scavenger?	Hopkins (1985)
Pseudorchomene plebs – McMurdo Sound, Southern Ocean	Phytoplankton aggregates, microzooplankton	Morphology (stomach contents)		Detritivore	Hopkins (1987)
Pseudorchomene rossi – Weddell Sea, Southern Ocean	Copepods, polychaetes, carrion	Feeding experiments and morphology (stomach contents)		Predator, carrion-feeder	Dauby et al. (2001)
Pseudorchomene rossi – Gerlache Strait, Southern Ocean	Planktonic crustacean remains (copepods, euphausiids), fish	Morphology (stomach contents)		Carrion-feeder, predator?	Hopkins (1985)
Pseudorchomene rossi – McMurdo Sound, Southern Ocean	Gelatinous zooplankton	Morphology (stomach contents)		Predator or scavenger on soft-bodied zooplankton	Hopkins (1987)
Swarms of amphipods – Mediterranean, 2800 m.	Phytodetritus	Video observations on phytodetrital bait	Undetermined	Detritivore	Jeffreys et al. (2011)
Unidentified lysianassoids – Northeast Pacific, bathyal	Large carrion	Lipid composition and fatty acids		Carrion-feeder	Drazen et al. (2008)

structuring and influencing the diversity of deep-sea communities; however, this view has recently been challenged (McClain and Schlacher, 2015), motivating us to propose several testable hypotheses for amphipod scavenger evolution. Building on the current state of knowledge on the biology and ecology of amphipod scavengers, we sketch a broader view of evolutionary ecology in the deep sea, based on which future research avenues could be developed.

3. Selection by competition: Food supply for scavengers in the deep sea

In this section, we discuss the wide array of food sources available to scavengers on the deep-sea floor (Fig. 1) and based on the literature at hand, we hypothesize how scavenging amphipods may locate them. The extent of competition within the scavenging guild depends on the regional variation of available food and the resulting selective pressure may favour generalists, specialists, or both. By giving on overview of what is known about the different detection mechanisms and feeding habits of scavenging amphipods, we argue that selection may have acted upon these stages in different ways; however, more research is necessary to find out how these account for the high diversity observed in scavenging amphipods.

3.1. *The food supply to the deep sea revisited*

3.1.1. *Export of primary production to the deep*

It is now established that seasonality at the ocean surface may be translated to the deep-sea floor within days or weeks. Given the degree of patchiness in productivity at the surface ocean indicated by satellite images of chlorophyll concentration, it is reasonable to assume equivalent, albeit diffuser, patterns reflected at the underlying sea floor (e.g. Pfannkuche et al., 1992; Smith et al., 1997). Primary production is either based on nutrients introduced to the surface layer by upwelling or deep mixing (new production) or on nutrients released there by the activity of bacterio-, protozoo-, metazooplankton and nekton (regenerated or recycled production). The upper limit of organic particle flux to the deep-sea floor is set by the magnitude of new production estimated at around 10–15 Gt yr^{-1} (Falkowski et al., 1998). New production regimes are generally dominated by chain-forming, often spiny diatoms that are known to form rapidly sinking aggregates after nutrient exhaustion (Smetacek, 1985). Fluffy layers of freshly sedimented diatoms on the sea floor have been observed in many regions of the deep sea (Beaulieu, 2003). Smetacek et al. (2012) estimated that at least 10 g C m^{-2} were deposited on the deep-sea floor in the aftermath of an experimental diatom bloom that was similar in magnitude to natural blooms. This is a substantial amount of carbon that can be visualized if converted into units tangible to us humans; thus 10 g C is equivalent to ca. 100 g living organic matter which would be the weight of a small fish filet, or 100 Antarctic krill or 100,000 *Calanus* copepods (Tande, 1982). Given the longevity of deep-sea benthos organisms, this amount of food can support a thriving benthic community of surface and infauna, including scavenging amphipods directly consuming fluff. Finally, abundant remains of coastal (seagrasses) and epipelagic (*Sargassum*) macrophytes have also frequently been encountered on the deep-sea floor, particularly in trenches, where they may sustain both generalist and specialist scavengers (Wolff, 1979; Grassle and Morse-Porteous, 1987)

3.1.2. *Sinking bodies of muscular zooplankton*

Muscular zooplankton, such as crustaceans and pteropods, tend to dominate biomass in productive regions through regular seasonal cycles (Verity and Smetacek, 1996). Diapausing copepods, typified by the dominant species of the boreal Atlantic, *Calanus finmarchicus*, build up biomasses of several g C m^{-2} during the growth phase after which the cohort descends, loaded with lipids, more or less *en masse* (Falk-Petersen et al., 2009), to the winter quarters at depths of 500 to more than 2000 m (Kaartvedt, 1996). In spring the cohort returns to the surface layer, attains sexual maturity, mates and lays eggs that establish the next generation (Falk-Petersen et al., 2009). This cohort survives traversing half the deep sea twice, no doubt suffering losses on the way, but retains sufficient numbers to maintain its status of dominant, regional copepod. Following reproduction, a sizeable proportion of the dead and sinking copepods is likely to reach the underlying sea floor, even at abyssal depths and this rain of dead copepods could well be

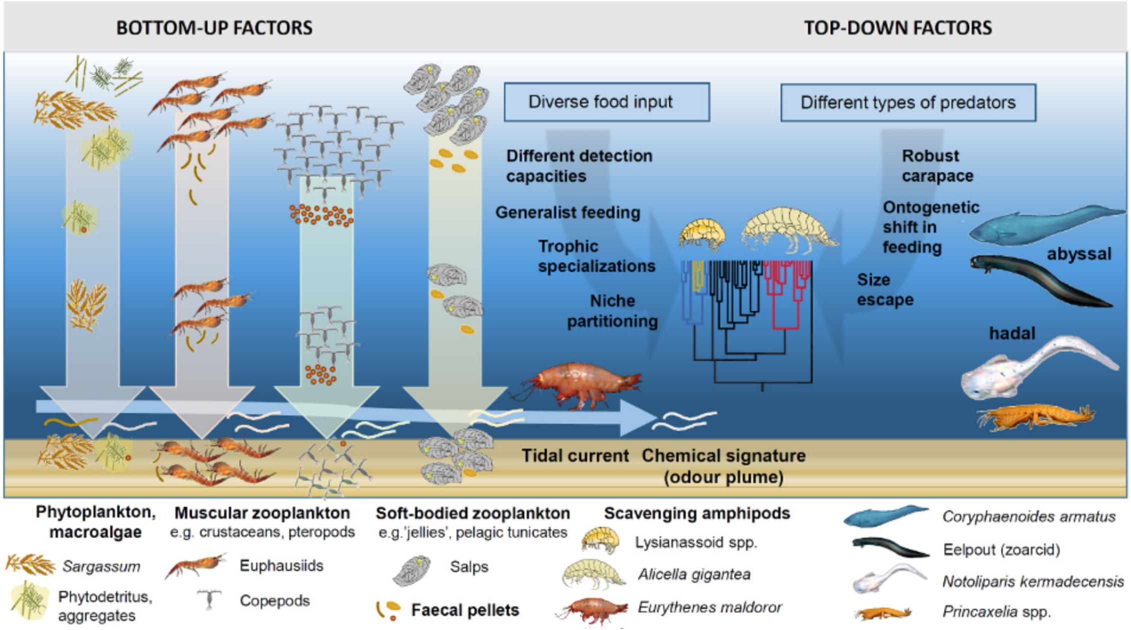

Fig. 1. Interplay of bottom-up and top-down factors on the diversification of amphipod scavengers in the deep-sea realm. The food input to the deep sea, ranging from phytodetritus, zooplankton to nekton and megafauna food falls (the latter not represented in this figure), its regional variation and the mechanisms of scavengers to locate food sources, may have favoured co-existence of generalist species with niche partitioning as well as specializations. Top-down factors (predation pressure), also varying locally and with depth, may have played a much more significant role in the evolutionary ecology of deep-sea scavengers than currently assumed, by favouring certain morphological and ecological traits. The different organisms are not to scale.

even more predictable than phytoplankton blooms. The importance of vertical migrations, diel and seasonal, in the export of carcasses and faecal material out of the euphotic zone to the deep-sea scavenging community has been emphasized (Wiebe et al., 1979; Angel, 1986), however the dead bodies themselves were previously not considered to be a predictable resource (Tyler, 1988). A significant fraction of the copepods found in a sediment trap moored at 70 m in the Canadian Arctic were identified as passively sinking copepods, representing 36% of the overall annual POC flux (Sampei et al., 2009), whilst their contribution increased to 91% in Arctic winter linked with copepod spawning events (Sampei et al., 2012). These observations support the hypothesis of a seasonally predictable copepod pulse as a significant food source for benthic scavengers.

In the case of other abundant muscular zooplankton such as euphausiids, pelagic amphipods and decapods, one can also invoke natural mortality at the end of life cycles. Crustacean food falls may be more common than widely believed and may represent, in some regions, a niche for deep-sea scavengers to specialize on. Natural processes include moulting failures and other environmental and trophic interactions that lead to injuries, losses of appendages or death (Kaiser and Moore, 1999). Since crustaceans moult seasonally or continuously depending on the species and their habitat, they may also represent a rather predictable source of carrion (Kaiser and Moore, 1999). A mass deposition at abyssal depths of swarm-forming swimming portunid crabs that died naturally, was reported from the Arabian Sea (Christiansen and Boetius, 2000), similar to that of euphausiid dead bodies that had presumably been at the end of the individual life cycle and observed to be fed upon by abyssal ophiuroid scavengers in the South Atlantic and Antarctic deep sea (Sokolova, 1994). The same may be true for other abundant taxa in subpolar and polar regions such as pteropods: gastropods of which several species bear snail-shaped aragonite shells. They can multiply rapidly and build up large biomasses particularly in high latitudes (Harbison and Gilmer, 1986). Their boom-and-bust life cycles imply that, although they are a favourite fish food, a large proportion of their population dies and sinks out at the end of their life cycle; because of the protection and ballast offered by their aragonite shells, a sizeable fraction of the sinking carcasses is likely to reach the deep-sea floor. Seasonal mass sinking of pteropods has been reported from sediment trap studies, for example in the Norwegian Sea at 100 m depth, where they represented in that period 8% of the annual carbon flux (Meinecke and Wefer, 1990; Bathmann et al., 1991). They were also recovered in deep-sea sediment traps from 200 to 2500 m in the Fram Strait (Bauerfeind et al., 2014) and 1000–2000 m in the Southern Ocean (Roberts et al., 2011), possibly representing an important food item for scavengers.

3.1.3. Sinking bodies of soft-bodied zooplankton

The large-volume, soft-bodied zooplankton comprises a heterogeneous group of organisms with convergent predator avoidance strategies: body volume is increased by storing large amounts of water in gelatinous tissue (e.g. siphonophores, scyphozoans), within bladder-like tunica (e.g. salps) or other devices (e.g. ctenophores). The combination of the generally low predation pressure with high growth rates of some species can result in massive blooms of “jellies” that have been reported, albeit sporadically, from many ocean regions (Boero et al., 2008). Once settled out on the sea floor, their carcasses can be dealt with at leisure by scavengers, whereby amphipods, with their grappling and tearing mouthparts, are particularly well adapted to feeding on them. “Jelly” carcasses are likely to have a short residence time so there are only few reports of their occurrence. High densities of giant jellyfish carcasses that died naturally have been reported from the seafloor at around 200 m depth in the Sea of Japan; they were colonized and consumed by scavenging invertebrates (Yamamoto et al., 2008). Similar observations of jellyfalls of the scyphozoan *Periphylla periphylla*, of which the biomass exceeded 50,000 tonnes in a single Norwegian fjord, have been reported on the deep-sea floor of this fjord (Sweetman and Chapman, 2011). Finally, soft-bodied zooplankton abundance on the continental shelf of the Northwest Atlantic appeared to be clearly linked with its consumption by fish scavenger species, showing that these surges of food may be important for the entire scavenging guild on the deep-sea floor (Smith et al., 2016).

Pelagic tunicates – appendicularians and salps – have in common that they often develop blooms of substantial biomass (Alldredge and Madin, 1982). They also both efficiently concentrate nanoplankton on fine-meshed filters. Given the abundance of their food supply, clogging of these filters can be a serious problem, which they have solved in different ways. Appendicularians can produce several new houses per day (Alldredge, 1977) whilst salps make new "individuals" by budding. The discarded appendicularian houses sink with rates of over hundred meters per day and are considered to be an important component of the biological carbon pump (Hansen et al., 1996). Whereas salp faeces are also believed to contribute substantially to vertical carbon flux (e.g. Pomeroy et al., 1984), the potential contribution of dead zooids has often been disregarded. Small salp carcasses (e.g. *Thalia*) have been reported neutrally buoyant and unlikely to sink to the deep sea, however, medium (e.g. the swarm-forming *Salpa fusiformis*) and large salps (e.g. *Thetys vagina*) may contribute large carbon fluxes to the benthos with their large faecal pellets and rapidly sinking carcasses (Wiebe et al., 1979; Henschke et al., 2016). Salp biomass can exceed densities of 100 t km^{-3} yr^{-1} (Tasman Sea, Henschke et al., 2013) and are characterized by high sinking rates of 165 – 253 m day^{-1} (Apstein, 1910). Mass depositions of salp carcasses have been observed both at bathyal (Henschke et al., 2013) and abyssal depths (Smith et al., 2014). The species *Salpa aspera* performs diel vertical migrations of over 800 m in massive numbers, and both its mortality and faecal production were calculated to meet the metabolic needs of the deep-sea benthos (Wiebe et al., 1979). Patches of high salp and doliolid abundances at ocean margins are considered rather predictable (Deibel and Paffenhöfer, 2009) and hence their occurrence as food falls on the deep-sea floor must be as well. Furthermore, it has been shown that the nutritional value of salps has been largely underestimated; eighty percent of their organic matter consists of protein (Madin et al., 1981), in the same range as that of phytoplankton blooms, copepods and fish (Henschke et al., 2013).

3.1.4. *Nekton and megafauna food falls*

A significant proportion of the biomass of all size classes of nekton – cephalopods and vertebrates larger than a few centimetres – is likely to sink to the deep-sea floor as a result of natural mortality. Open ocean swarm-forming, small and medium-sized fish (e.g. clupeids and scombrids) have a life-span of only several years and are characterised by mass spawning events (King and McFarlane, 2003). Larger animals not only have a lower mortality, they also have fewer predators that can swallow them in one gulp, hence a greater proportion of the biomass of adult individuals will die of senescence and injuries and sink rapidly to the sea floor. This applies particularly to the open ocean where a dead, or even severely wounded, member of the megafauna – from sunfish to tuna and whales (Norman and Fraser, 1938) – will immediately start to sink at high rates. One could expect a larger outfall of dead and dying large fish to the sea floor on spawning grounds than on the feeding grounds, especially in the case of animals that die after spawning. Mass mortality after spawning is a distinguishing and well-known characteristic of salmonids because they spawn in shallow waters (e.g. capelin) or rivers (salmon, etc.). Pelagic fish species such as sardines and anchovies, spawn in the open ocean and are likely to share the same fate with the difference that spent individuals will escape notice by sinking to the deep-sea floor. The majority of nektonic squid species are known for their rapid growth and their semelparous reproduction, with females dying after the spawning event. As an example, the short-finned squid *Illex argentinus* spawn at an age of one year, after which they die *en masse* over the slope, estimated at 0.5 million tonnes of biomass (Arkhipkin, 2013). These regions must be characterized by a reliable supply of sinking carcasses, representing a huge biomass during the squid spawning season on which many scavengers can feed. Studies on fisheries discards have taught us that most of the large animals composing the trawlers' discards (e.g. crustaceans, echinoderms, cephalopods, turtles, sharks) sink to the bottom within minutes (Hill and Wassenberg, 1990). Over the deep sea, a megafaunal carcass, or its more substantial parts, could land on the sea floor within an hour after death in the surface. The only interceptors capable of halting a sinking megafauna, or piece of it, are squid and pelagic octopuses; deduced from the biomass of their known predators – large toothed whales – deep-sea cephalopod biomass must be quite substantial and accordingly their food supply. Unlike fishes and whales that eat by the mouthful, cephalopods can grab hold of a large prey item, keep it in suspension and eat it at leisure with minimum energy expenditure. So except the carcasses intercepted by cephalopods, most large nekton and megafaunal carrion will provide food for a large scavenging guild on the deep-sea floor for long periods. For example, large fish falls, such as mobulid ray and whale shark carcasses, have been reported from the deep-sea floor on the Angola continental margin, providing food for scavengers for extended time periods from weeks to months (Higgs et al., 2014). At least ten distinct lysianassoid species have been reported from baited traps in this area, caught in very high numbers, corroborating the fact that food falls are abundant in this region (Duffy et al., 2016). Whale mortality and flux of carcasses to the seafloor is tenfold greater along migration corridors or in feeding grounds, which generally represent productive regions such as oceanographic fronts or along ocean margins (Smith, 2006). Within the north Pacific gray whale range, whale falls occur annually with an average nearest neighbour distance of less than 16 km, supporting the mobile scavenger stage, including the lysianassoids, for several years (Smith and Baco, 2003). Blue whale carcasses can support scavengers for as long as 7 – 11 years (Smith, 2006).

3.2. *From trophic plasticity to specializations: clues for diversification events in the deep*

We have argued above that the deep-sea habitat offers much more scope for feeding than implied in the belief 'the energy supply of scavengers is restricted to unpredictable, sporadic large food falls'. Hence, other, highly specialized feeding adaptations may have evolved within the scavenging guild comparable to the well-known example of the whale bone worms *Osedax* (Glover et al., 2013). Some species may be specialist scavengers adapted to feeding on particular types of food falls, however, a large proportion are likely to be generalists, exploiting the broad array of food falls landing on the seafloor: from feeding on phytodetritus and other particles on the sediment surface to dead zooplankton and nekton extending on to predation on other animals on the sea floor or in the water column. Smaller-sized taxa (e.g. *Abyssorchomene*, *Orchomenella*, *Uristes*) are believed to be facultative necrophages, processing food less efficiently than the larger-sized genera such as *Eurythenes*, *Alicella* but also *Hirondellea*, thought to be obligate scavengers of large food falls based on their morphological and physiological adaptations to necrophagy (mandibles, gut storage capacity, low metabolism; e.g. Dahl, 1979; De Broyer et al., 2004). Ecological studies have shown that this differentiation no longer holds true since both groups of amphipods seem to use a variety of food sources, summarized in Table 1. *E. gryllus* displays alternative feeding strategies such as predation (Templeman, 1967), ingestion of mud (Barnard, 1962) or phytodetritus from the sea floor, that even vary seasonally concomitant with surface productivity (Janßen et al., 2000). A shift to alternative food sources may also provide an explanation for camera observations of individuals swimming near a bait without being attracted to it (Smith and Baldwin, 1982), which seems unlikely to happen in the case of starving animals entirely dependent on large carrion. Finally, lysianassoid scavengers are also attracted to macrophyte food falls (e.g. *Sargassum*) (Lawson et al., 1993, Table 1) and known to feed on them in regions where they are abundant, even at abyssal depths, such as in the Sargasso Sea (Grassle and Morse-Porteous, 1987; Fleury and Drazen, 2013) or where they accumulate in topographic features such as submarine canyons (Vetter and Dayton, 1999).

Whilst co-existing generalist scavengers can well occupy different niches, as shown for shallow-water crustaceans (Tran, 2014), niche partitioning between both generalist and specialist scavengers may have led to speciation and diversification events in the different scavenging groups. As shown for subterranean amphipods, morphologically cryptic sister species can in fact occupy very distinct feeding niches ranging from predation to filter-feeding (Fišer et al., 2015). The role of competition-driven specialisation in divergence could be investigated with a detailed study on the feeding morphology and habits of the various species recently uncovered in the species complex *Eurythenes*, for example (Havermans, 2016). Camera or trap studies in the deep sea have used mostly large fish and occasionally squid as bait, but only a few studies have provided smaller organisms such as soft-bodied zooplankton. Recent trap studies showed that amphipod scavengers attracted by the classical fish-filet baits also visited baits of jellyfish and efficiently devoured these in a few hours (Sweetman et al., 2014). Regional variations in the function of the scavenger guilds could be studied and each component classified according to their role in the consumption of food falls based on experimental work and diet analyses. Having entered the "OMICS"-era, we can explore genomes, transcriptomes and metabolomes for indications of adaptations to a diverse food supply at population and species levels.

As an example, *Hirondellea gigas* is able to digest cellulose and hemicellulose, and it is believed that this species feeds on sunken wood or plant debris (Kobayashi et al., 2012). Interestingly, no lignase activity could be observed in *H. gigas* and their guts were filled with sediment whilst no wooden debris was found (Kobayashi et al., 2012). Hence, this may represent an adaptation evolved to feed upon the mass sinking soft bodies of tunicate organisms. Tunicates are unique in the animal kingdom for their ability to biosynthesize cellulose (Brown, 1999). The outer coverings or tunica of the former groups are long known to contain cellulose; more recently appendicularians have been shown to have cellulose fibrils in both the tail (Sagane et al., 2010) and in the houses (Kimura et al., 2001). Soft-bodied carcasses of tunicates would have digested rapidly and might have been overlooked, but molecular analyses offer the possibility to detect minute quantities of tunicate tissues, which has been shown for hadal *E. gryllus* populations (Blankenship and Levin 2007, Table 1). In these hadal specimens, stomachs contained tunicate DNA, confirming it to be a common resource on the sea floor. Whether this cellulase enzymatic activity evolved solely in this species or in several lysianassoid lineages needs to be further examined. The latter seems more likely since endogenous cellulases are more widespread in invertebrate taxa than previously thought, after being reported in crustaceans, ascidians and molluscs (Lo et al., 2003).

3.3. A mixture of odour plumes transported by tidal currents

3.3.1. Tidal currents as vectors of chemical cues for swift scavengers

Detection of large food falls by amphipod scavengers has been hypothesized to be both chemical and mechanical (Klages et al., 2002). Cuticular structures, named sensilla, often concentrated on the posterodorsal body surface, are believed to be responsible for chemical detection (e.g. Steele, 1991) and hydrodynamical sensory information, allowing the animals to orient themselves in currents (e.g. Olyslager and Williams, 1993). The lysianassoid amphipod *Anonyx* has a very large number of these specialized chemosensory sensilla compared with other, non-lysianassoid, amphipod species. These sensilla are concentrated where the drag-force of current flow generated by swimming when the body is extended, and in the pathway of the microcurrents generated by the beating of the pleopods (or swimming legs) when in a curled-up position, will be greatest (Steele, 1991). For chemical detection, amphipods also possess specialized sensory organs shaped as a bundle of setae – the callynophores – located on the antennules that are believed to be responsible not only for detecting receptive females but also for food detection in both sexes (Dahl, 1979).

Scavenging shallow-water amphipods have been observed swimming along the bottom with a back-and-forth sweeping pattern, frequently changing direction, in order to localize chemical cues or attractants (Busdosh et al., 1982). Others have been observed swimming in straight lines in random directions (Ide et al., 2007), spirals (Smith and Baldwin, 1982) or cross-stream patterns (Sainte-Marie, 1986), to enhance the chance of detecting an odour plume. When the chemical signature of the bait itself has been detected, amphipods swim up-current following the odour plume towards the bait (Premke et al., 2003), which are believed to be detected over distances of several kilometres (Ingram and Hessler, 1983). The signal is amplified when the first amphipod starts penetrating the skin and reaches the flesh which releases substances from the punctured carcass or when it excretes substances itself during feeding that will enhance the recruitment of new scavengers, and facilitate their access to the carcass. This phenomenon explains the commonly observed cluster of amphipods, aggregating on the same fish in large numbers whilst another adjacent one can remain untouched. The analogy with vultures hovering with air currents suggests that scavenging amphipods also passively drift with water currents above the seafloor in order to survey large areas for benthic carcasses (Ruxton and Houston, 2004). First, with the exception of benthic storms, currents are rather sluggish in the abyss and second, in order to locate carcasses following their chemical cues, amphipods need to swim against the current. A more sensible scenario would thus be similar to the one proposed decades ago (e.g. Hessler and Jumars, 1974; Thurston, 1979) of a scavenger amphipod sitting on the seafloor or swimming slowly, that, upon detection of chemical stimuli carried by tidal currents, will initiate rapid swimming up-current to locate the carrion source. Tidal currents have been frequently measured in both the bathyal and the abyssal zones; they vary between 2 and 15 cm s^{-1} (Lampitt and Burnham, 1983; Jones et al., 1998; Janßen et al., 2000; Kemp et al., 2006) and change direction on average every 5–6.5 h (Kemp et al., 2006). In this case, scavengers need to be swift to locate and arrive at the carrion, before tidal currents change direction. However, amphipods were observed to relocate the bait when currents change: after having lost the scent plume, they switched back towards the searching mode – swimming back and forth, until exposed to a certain threshold of the attractant when uni-directional up-current swimming was re-initiated (Busdosh et al., 1982). Rapid arrival at bait has often been demonstrated, with record arrival time in shallow waters of several Antarctic scavenging amphipods of only ten minutes (Bregazzi, 1973), or the first individual after only five minutes at depths around 9600 m in the Philippine Trench (Hessler et al., 1978).

There is evidence that numbers of deep-sea fish, shrimp and amphipod scavenger species at bait are correlated with tidal cycles, but a clear common trend could not be identified since abundances at baits of some taxa were positively related to current speeds whilst others negatively, or not at all (e.g. Lampitt et al., 1983; Moore and Wong, 1996). Arrival time depends not only on current speeds but also scavenger density and duration of attraction. Swimming up-current will survey a longer distance than down-current but if an individual were only to swim up-current over an entire tidal cycle, it would swim back and forth and lead to residence within a restricted region – a classic red queen situation. To move to a new geographical location, the animal would have to swim up-current only in the same direction, for instance according to the geomagnetic field given the presence of specific sensors, or for one phase only in each tidal cycle. In shallow waters, the activity of scavenging amphipods has been linked to the tidal cycle in several instances (e.g. Sainte-Marie, 1986). In the deep sea, one can imagine that a meshwork of horizontal and vertical swimming patterns could also be optimised for the local tidal currents that swing back and forth about twice a day.

3.3.2. "Scent-sitivities" differ amongst scavengers

The nature of the chemical cues or attractants can play an important role in the detection capacities, and hence the feeding preferences of the different scavenger species (e.g. Ide et al., 2006). In contrast to the terrestrial environment where only volatile substances transport odour, any soluble substance in water is a potential attractant. Moreover, dispersion of substances in water is slower by five orders of magnitude than in air, remaining detectable over a longer time and distance (Csanady, 1973). Similarly, density surfaces last longer in water than in the air, where turbulent mixing is much stronger. Logically, the concentrations of attractants in the surrounding water allowing the scavenger to detect food will depend on their emission from the source, the subsequent turbulent mixing into the surrounding water and their advection and dispersion (Westerberg and Westerberg, 2011). The initial odour in a plume will be proportional to the concentration at the carcass or bait, and inversely proportional to the current velocity. Experiments have shown that, due to the low diffusivity, the initial concentration of attractant is not dependent on the size of a solid bait but rather on the ratio of the surface to the cross-section area of the bait (Westerberg and Westerberg, 2011). Thus, a solid bait cut into pieces with irregular shapes will release the most attractant. Furthermore, the effect of the current speed on the initial dilution is such that the maximum plume concentration occurs at slack tide even if this occurs several hours after the setting of the bait (Westerberg and Westerberg, 2011). Scavengers can therefore not reliably estimate the size of the carcass by the concentration of an odour plume since the latter depends on a combination of the carcass' shape, the current speed and soak time (Westerberg and Westerberg, 2011), hence it is rather the nature of the chemical signature itself that will allow the scavenger to differentiate between types of food falls.

It is long known from shallow-water environments that free amino acids stimulate crustacean and fish chemoreceptors and trigger feeding behaviour (Mackie and Shelton, 1972; Fuzessery and Childress, 1975; Hara, 2006). Combinations of amino acids are stronger attractants than singles, which has been confirmed with laboratory experiments with lysianassoid amphipods (Ide et al., 2006). The extent to which these attractants induce locomotion – or foraging – depends on the strength of the signal relative to the background concentration (Ide et al., 2006). The threshold concentration inducing foraging seems not only to vary between crustacean groups (decapods and amphipods) but even between closely related amphipods, depending also on the background concentration. The threshold concentrations of amino acids were around 10^{-7} mol L^{-1} for the shallow-water lysianassoid *Aroui onagawae* (Ide et al., 2006) much lower than those of *Orchomene limodes* of 10^{-5} mol L^{-1} (Meador, 1989). This agrees with the hypothesis that *A. onagawae* is a fast-swimming scavenger and active suprabenthic forager (Ide et al., 2006, 2007), whilst *O. limodes* is a smaller, less mobile and crawling, facultative, scavenger (Meador, 1989). Furthermore, the latter reacts only to certain amino acids, only present in substantial amounts in animal tissue (e.g. taurine, tryptophane) whilst the former is able to distinguish ubiquitous amino acids, abundant in tissues of almost all marine animals (e.g. glycine, alanine, arginine) (Ide et al., 2006).

Some terrestrial and aquatic animals recognize the chemical substances, also called necromones, produced by death and decomposition of dead organisms. If these unsaturated fatty acids, oleic acids and linolenic acids are to be distinguishable at a specific level, scavengers may have developed an olfactory capacity to recognize the type of decomposing food falls, likely inducing specialized or preferential feeding behaviour. Several studies have shown a preference of scavengers for teleost fish and other carrion compared with elasmobranch carcasses, with the latter being consumed at ten-fold lower rates (Witte, 1999; Janßen et al., 2000; Higgs et al., 2014), hypothesized to be due to their tough skin deterring smaller scavengers such as amphipods and their necromones repelling the Portuguese dogfish (*Centroscymnus coelolepis*), a major large scavenger in the area. However, only mega-carrion will "stink" over time: smaller food falls are likely to be consumed by scavengers more rapidly before anoxia by bacteria can occur and release the characteristic carrion smell. However, also the smaller carcasses, e.g. those of crustaceans, must have their own chemical signature that can be detected by scavengers, like in the case of *Tryphosa nana*, attracted only to crab carcasses (Moore and Wong, 1996).

4. Selection by predation: Morphological and ecological adaptations

There is increasing evidence that marine organisms invest considerable resources to avoid being eaten and that top-down selection has been equally or more important in dictating their evolutionary trajectories than bottom-up factors such as competition for resources (Verity and Smetacek, 1996; Smetacek, 2012). The paradigm that predation does not increase diversity in deep-sea assemblages has recently been challenged by McClain and Schlacher (2015); however, top-down effects in the deep-sea realm remain virtually unknown. Despite the little information available on the importance of predation pressure on deep-sea crustaceans, it has been hypothesized to play a major role in shaping the size distribution of juveniles and adults, with smaller life stages being more vulnerable to predation or 'cropping' by macro- and megafaunal organisms (Wilson and Ahyong, 2015).

Amphipod scavengers feeding on large food falls are numerous and vulnerable to predation. Since they are known to stay, often motionless, on a carcass or bait for hours or even days, they need to be well protected against fish that could simply pick their prey from the amphipod 'brochette'. The gluttonous feeding of amphipods at food falls seems to induce moulting to ensure a larger storage capacity, a hypothesis which would explain the large number of empty exoskeletons observed in baited traps (Ingram and Hessler, 1983, Thoen et al., 2011) – if true, this would render them even more vulnerable to predation. Several bathyal and abyssal fish species are attracted to large food falls to feed on scavenging amphipods, such as liparids (e.g. *Paraliparis bathybius,* Lampitt et al., 1983), grenadiers such as *Coryphaenoides (Nematonurus) armatus* (Jones et al., 1998), and zoarcids (eelpouts) such as *Pachycara* species (Higgs et al., 2014). The latter are often observed roosting around food falls as well as generating long deep grooves in the carcass to feed on flesh-boring amphipods (Witte, 1999). Scavenging lysianassoids, such as *Eurythenes*, have been found in the stomachs of macrourid species (*C. armatus*, Pearcy and Ambler, 1974, *Macrourus carinatus*, Jones, 2008). Since the fish assemblages occurring at food falls differ between the type of food falls (Jones et al., 1998) and their locality, the resulting selection pressures will also vary, with a potential for local morphological and/or ecological adaptation of their prey.

It was believed that amphipod populations may be less controlled by fish predation in the hadal zone, due to the logarithmic decline in the number of fish species with depth (Priede et al., 2006). Hadal zones differ significantly in terms of overlying surface productivity regimes and hence this general trend can only be explained by the pressure regime, or by the aforementioned shift in size spectrum of the sinking particles. The decline in fish abundances may explain the ten-fold increase in abundance of scavenging amphipods between 6000 and 10,000 m depth (Jamieson et al., 2009a). Nonetheless, endemic liparid fishes from hadal trenches have been observed to occur in high numbers (Fujii et al., 2010) and actively feeding on mobile scavenging amphipods. For example, *Pseudoliparis amblystomopsis* and *Notoliparis kermadecensis* fed on small (1–2 cm) scavenging amphipods by suction feeding and not on the bait (Jamieson et al., 2009a). Furthermore, predation on scavenging amphipods by decapods (Jamieson et al., 2009b) and by other large predatory amphipods, such as the pardaliscids *Princaxelia* spp. (Jamieson et al., 2012) seems to be prevalent in the hadal zones, particularly at depths below 8000 m.

4.1. Heavy-duty armour

As most benthic animals, amphipods have invested in armour for deterring rather than body musculature for escaping predators. Typical examples can be found in the Baikalian amphipod fauna with its highly armoured forms belonging to the endemic family Acanthogammaridae (Kamaltynov, 1999). The family Epimeriidae comprises a particularly high species number in the Southern Ocean, well-known for its characteristic variety of dorsal carination, spines and teeth which is

Fig. 2. Overview of different amphipod scavenger morphologies. Upper photograph: the deep-sea supergiant *Alicella gigantea* (Alicellidae), scale bar = 2 cm, copyright A. Jamieson, Oceanlab, University of Aberdeen. Middle photograph: one of the several giant deep-sea amphipod species of the *Eurythenes* complex, *Eurythenes maldoror* (Lysianassoidea: Eurytheneidae), scale bar = 1 cm, copyright M. Schneider, Senckenberg Research Institute. Lower photograph: a common carrion-feeder of the Antarctic shelf and slope environment, *Waldeckia obesa* (Lysianassoidea: Lysianassidae), scale bar = 0.5 cm, copyright C. d'Udekem d'Acoz, Royal Belgian Institute of Natural Sciences.

hypothesized to originate from a predator-prey co-evolution with notothenioid fishes (Brandt, 2000). In contrast to these examples, the general *bauplan* of scavenging shallow-water and deep-sea lysianassoid amphipods is remarkably conservative: spines and teeth are absent. In analogy to the naked necks of vultures with which they efficiently probe carcasses, dorsal teeth and spines would hinder the entering and tunnelling of amphipods in large carrion. Lysianassoids are known to enter carcasses through incisions or body openings, mining the muscle tissue between the skeletal structures of bony fish or between the connective tissue, skin and blubber in the case of cetacean carcasses (Jones et al., 1998).

Hence, scavenging amphipods have developed alternative defence strategies. The body musculature is particularly reduced, compromised by an expandable gut and increased lipid storage capacity. Instead of developing escape muscle, as is typically the case in copepods and euphausiids (Verity and Smetacek, 1996), scavenging amphipods (most lysianassoids and allicelids) clearly invested in evolving an armature composed of a strong chitinous cuticle, large coxal plates, spiny posterior legs and telson and a compact body made for burrowing (Fig. 2). When confronted with danger, *Waldeckia obesa* (Fig. 2), an obligate carrion-feeder inhabiting both littoral and deep-sea waters, rolls into a ball rather than escaping, apparently relying on its strong cuticle as defence (Chapelle et al., 1994). With its heavy armature, it is also rejected as food by notothenioid fish (Fanta, 1999) that are the major amphipod predators on the Southern Ocean shelf, corroborating its efficiency as predator defence. Gathered closely together whilst feeding on food falls, amphipods are often found with only the posterior part of their body exposed, their spiny uropods and telson might deter their predators.

4.2. Size escape: Giants and supergiants

In the deep sea, two conspicuously large-sized genera exist: *Eurythenes* and the monotypic *Alicella* (Fig. 2). These so-called giant and supergiant amphipods, reach body lengths of 14 cm and 34 cm, respectively, as opposed to the majority of the scavenger amphipods with sizes of ca. 1 cm. It has been hypothesized that natural selection will have favoured a higher ability to consume large volumes of food at a single meal and hence, larger sizes, however, we believe that these cases of gigantism represent a size escape rather than an adaptation linked to surviving longer periods of starvation, which seems to be equally possible for smaller-sized amphipods (e.g. *Paralicella*). Fish and predatory crustaceans preferentially consume mid-sized amphipods (~1.5 cm, Jamieson et al., 2009a,b). Several smaller bait-attending predators, such as the abyssal liparid fish *Paraliparis bathybius*, have a mouth gape that excludes the ingestion of any but the smallest juveniles of *Eurythenes*, mainly consuming smaller lysianassoids such as *Paralicella* and *Orchomenella* (Lampitt et al., 1983). In the hadal zone, predation pressure by fish species is believed to be more relaxed compared with the bathyal and abyssal zones (even though feeding by suction on individual amphipods has been noted by hadal liparid fish; Jamieson et al., 2009a) and other predators seem to be more prevalent such as large predatory amphipods (10 cm, Jamieson et al., 2012) and decapods (15–23 cm, Jamieson et al., 2009b). Considering that *Eurythenes* and *Alicella* belong to different families, the Eurytheneidae (Lysianassoidea) and Alicellidae respectively, size escape or gigantism appears to have evolved twice independently in the evolution of scavenging amphipods. These big animals seem to invest in armour compared to musculature, with thick carapaces of a high chitinous content. Sampled specimens of *A. gigantea* resembled an empty exoskeleton with few muscles; the cavity is most likely filled by the significantly expanding gut after feeding. Even though *Eurythenes* has strongly developed pleopods for swimming, the cumbersome armour comes at a price: most of the much smaller lysianassoids swim faster. Whilst *Eurythenes* has been recorded at swimming speeds of only 1.3 bodylength s^{-1} (Laver et al., 1985), smaller shallow-water lysianassoids such as *A. onagawae* have been reported to swim as fast as 16 L s^{-1} although in other species it usually varies between 5 and 10 L s^{-1} (reviewed in Ide et al., 2007). Differences in the armature might result from differences in predation pressure by larger predators, depending on the region and depth. For example, *E. sigmiferus*, a newly described species, differs from its congeners in the development of a dorsal carination (d'Udekem d'Acoz and Havermans, 2015) that may find its origin in predation defence.

4.3. Hiding in the three-dimensional and the deep-sea floor as a kindergarten?

In the case of several shallow-water lysianassoids, foraging activity is limited to the periods of darkness; during daylight they often reside motionless on the sea floor, swim close to it or burrow in the sediment (for a summary see Ide et al., 2007). Some species even rest in large numbers as a tight clump adjacent to rocks (Ide et al., 2007). In the deep sea, many scavengers are benthopelagic, illustrated by the giant and mobile *Eurythenes* species, extending their habitat far above the seafloor and residing in the pelagic realm. Not only different species (Duffy et al., 2012), but also intraspecific life stages (e.g. Eustace et al., 2016) are able to partition their environment by carrying out ontogenetic migrations in the water column. With the evidence of pelagic feeding, these migrations have been explained as an alternative feeding opportunity rather than escape from predation (Smith et al., 1979). Amphipod predators such as rattails (e.g. *C. armatus*) have been recorded at several hundreds of meters off the sea floor feeding on pelagic prey (Smith et al., 1979). Despite the presence of predators in the water column, dispersing in overlying water may provide a higher chance for survival than residing on the rather featureless deep-sea floor. Whether ontogenetic migration of *Eurythenes* has its origin in predation escape, in particular by ovigerous females, or in finding food as predators, should be further investigated. Finally, females of *Eurythenes* are believed to descend to the sea floor to release their hatchlings. All juveniles so far investigated were fully capable of an independent existence, with functional mouthparts and pleopod characteristics developed for swimming (Thurston and Bett, 1995), which indicates a high degree of extended parental care, likely as an adaptation for reducing predation pressure on the juvenile stages. One *Eurythenes* female releases more than 200 hatchlings (Thurston and Bett, 1995) which would be able to start feeding on the deep-sea floor just after release, or burying into the sediment feeding on infaunal organisms. In that case, the deep-sea sediment could offer both food and protection for the newly hatched juveniles.

5. The marine scavenger fauna in the Anthropocene

It is worth mentioning here that, in analogy to the decimation of marine megafauna over the last centuries, the bulk of the terrestrial megafauna became extinct over all continents and islands except Africa and parts of South Asia by the beginning of the Holocene. The effects on vulture populations have been drastic as well; the American condors are the only survivors of very large species that ranged up to 70 kg body weight and wing spans of 6–8 m (Campbell, 2015). The fact that such large carrion-feeders evolved suggests that there were correspondingly huge megafaunal species populating large regions with a surprisingly high biomass density by current standards. One is reminded of reports describing the enormous density of whales in the Southern Ocean prior to their decimation (Mackintosh and Wheeler, 1929) as well as those describing the extraordinary numbers of whales seen in other regions not yet reached by whalers (e.g. Shelvocke, 1726; Hackluyt, 1904; Hoare 1982). The early observations have been corroborated by genetic evidence showing that pre-whaling populations were far greater than present-day population estimates (Roman and Palumbi, 2003). Britton and Morton (1994) speculate that large food falls will have been rare prior to industrial fisheries because they assumed that the bulk of pelagic animal biomass was consumed within the water column. The authors warned that current shallow-water and deep-sea scavenger stocks might well have increased over the past century due to human intervention by provision of bycatch and processing remains or discards. We hold the opposite view and argue that several resources for scavengers, e.g. whale, nekton and wood falls, have decreased enormously under anthropogenic pressure. As argued above, significant proportions of plankton and nekton species populations are likely to have died of senescence and sunk to the deep-sea floor instead of all being consumed by predation. Therefore, on the one hand, overfishing, similar to whaling (Smith, 2006), by reducing the overall stock biomass, has had and will continue to have catastrophic negative impacts on carrion-feeders, in particular those depending on nekton carcasses. One can also anticipate shifts in the structures of pelagic ecosystems caused by climate change, overfishing and other anthropogenic forcing that will also impinge on the deep-sea fauna in unforeseen ways. There is an extensive literature on regime shifts in pelagic ecosystems (Möllmann et al., 2015, Conversi et al., 2015) that provides an insight into the nature of the wide-ranging discussion. The ongoing debate on the effect of overfishing on pelagic food webs is an example, with a hypothesized world-wide increase in gelatinous zooplankton (Hamilton, 2016). On the other hand, marine fisheries have enormous bycatches and discards – in terms of millions of metric tons of carrion – that in the decade-scale period of nekton decimation will have enhanced carrion supply. However, these anthropogenic food falls are mostly concentrated in coastal and productive areas with less effect on open-ocean, deep-sea scavenging communities.

Despite its vastness and apparent inaccessibility, the deep sea is and will be increasingly impacted by anthropogenic activities, of which the consequences are hard to predict – hampered by the poor knowledge of the system and its functioning. Motile scavengers are identified as one of the target groups for studying the effects of deep-sea mining activities (International Seabed Authority, 2010). Although their ecology is not yet well understood, the effect of mining will likely strongly differ from that on other components of the deep-sea fauna. As already stated by Jumars (1981), it would be useful to know the sources, rates and intensities of natural disturbances in order to predict those of the anthropogenic ones which the scavenger populations may face but on a wider scale. In the light of all anthropogenic influences, one wonders how trophic strategies and population densities of scavenger assemblages have changed in the course of the Anthropocene and will do so in the next decades. There is an urgent need to establish qualitative and quantitative baselines for comparative purposes in different regions of the deep sea; international, interdisciplinary research programmes could provide a framework to develop and apply adequate instrumentation and standardised methodology to test hypotheses on global deep-sea evolutionary ecology such as those formulated by Danovaro et al. (2014) and McClain and Schlacher (2015). Finally, genomic tools may elucidate the demographic histories and past bottlenecks of certain populations in a particular region and link these with past anthropogenic influences, such as the decimation of the major megafauna populations or fish stocks inhabiting the area.

6. Conclusions

The fact that there existed, prior to the depredations of industrial fisheries, huge stocks of adult, breeding fish (Jackson et al., 2001) indicates that predation pressure on the adults of what eventually became commercial fisheries must have been low enough to enable a significant proportion of the populations to reach their species-specific age limit, die somewhere in the water column and then sink to the underlying sea floor at rates dictated by Stoke's law. Various species of zooplankton, particularly those with boom-and-bust life cycle strategies such as salps, pteropods and jellyfish are also likely to perish in the upper layers and sink *en masse* to the deep sea floor albeit more slowly at rates of hundreds of meters per day. Since their lifetime on the sediment surface is likely to be short, carcasses of smaller zooplankton to smaller-sized fish or squid, will not feature in deep-sea video footage the way diatom fluff or a whale carcass would. The amount of food reaching the deep-sea floor depends on processes occurring in the surface layer such as the type of phytoplankton, e.g. diatom or flagellate, zooplankton and nekton. Consideration of all these possible sources of food provides room for a broad range of feeding types in the sediments not very different to the complex food webs typical of continental shelves. We argue that mobile, scavenging amphipods are amongst the best adapted organism groups to utilize these various food sources in different ways; they are accordingly likely to be a major food item of the deep-sea predator chain. Although they are ubiquitously present, their global abundance and biogeography, local densities and population sizes are not well known because of the difficulties associated with standardizing and adequately interpreting the point measurements that represent the baited trap deployments with which they are sampled. We propose baited trap studies using various types of food – from soft-bodied or muscular zooplankton to macrophytes, large fish falls and mammals – to explore foraging behaviour, feeding habits and prey preferences of motile scavengers. The role of currents in carrion detection and the densities of scavenging populations could be monitored with video stations and standardized baited trap deployments to compare populations across a depth or productivity gradient, subject to distinct "rhythms" (various tidal regimes, monthly, seasonal or annual periodicities) or under different predation pressures or food regimes. Marine protected areas could well serve as experimental sites to study the long-term effect of rebuilding nekton populations on carrion feeders. Diet studies based on biomarker (stable isotopes, fatty acids) and molecular (e.g. high-throughput sequencing) analyses will contribute to shedding light on the actual diversity of feeding habits of scavenging amphipods across the variety of deep-sea habitats and along the different depth gradients. Yet unknown feeding specializations could be discovered by detailed examinations and comparisons of the mouthparts of distinct amphipod populations and linked with the availability and types of food fall that they are most likely to encounter in these regions. Hypotheses of possible co-evolutionary pathways with the diversification of particular megafaunal groups and trophic shifts or population bottlenecks or expansions linked with the depletion versus the explosion of certain resources in the course of the Anthropocene can be tested with the most modern molecular methods. Thorough "omics"-studies based on a comprehensive sampling set across taxa and oceanic basins – from the polar regions to the tropics– will allow us to delve deeper into the evolutionary history and ecology of this group that is so characteristic of the entire World Ocean.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.pocean.2018.04.008.

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