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The biological effects of ionising radiation on Crustaceans: A review

Neil Fuller[a], Adélaïde Lerebours[a], Jim T. Smith[b], Alex T. Ford[a],*

[a] *Institute of Marine Sciences, School of Biological Sciences, University of Portsmouth, Ferry Road, Portsmouth, Hampshire PO4 9LY, UK*
[b] *School of Earth & Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth, Hampshire PO1 3QL, UK*

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ABSTRACT

Historic approaches to radiation protection are founded on the conjecture that measures to safeguard humans are adequate to protect non-human organisms. This view is disparate with other toxicants wherein well-developed frameworks exist to minimise exposure of biota. Significant data gaps for many organisms, coupled with high profile nuclear incidents such as Chernobyl and Fukushima, have prompted the re-evaluation of our approach toward environmental radioprotection. Elucidating the impacts of radiation on biota has been identified as priority area for future research within both scientific and regulatory communities. The crustaceans are ubiquitous in aquatic ecosystems, comprising greater than 66,000 species of ecological and commercial importance. This paper aims to assess the available literature of radiation-induced effects within this subphylum and identify knowledge gaps. A literature search was conducted pertaining to radiation effects on four endpoints as stipulated by a number of regulatory bodies: mortality, morbidity, reproduction and mutation. A major finding of this review was the paucity of data regarding the effects of environmentally relevant radiation doses on crustacean biology. Extremely few studies utilising chronic exposure durations or wild populations were found across all four endpoints. The dose levels at which effects occur was found to vary by orders of magnitude thus presenting difficulties in developing phyla-specific benchmark values and reference levels for radioprotection. Based on the limited data, mutation was found to be the most sensitive endpoint of radiation exposure, with mortality the least sensitive. Current phyla-specific dose levels and limits proposed by major regulatory bodies were found to be inadequate to protect species across a range of endpoints including morbidity, mutation and reproduction and examples are discussed within. These findings serve to prioritise areas for future research that will significantly advance understanding of radiation-induced effects in aquatic invertebrates and consequently enhance ability to predict the impacts of radioactive releases on the environment.

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* Corresponding author.
E-mail address: alex.ford@port.ac.uk (A.T. Ford).

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1. Introduction

The renewed interest in nuclear power as a low carbon emission energy source coupled with concern regarding past and potential nuclear accidents dictate that elucidating the impact of radionuclides on the environment is a global issue. Traditional approaches to radiological protection of the environment are based on the assumptions that the standards of environmental control needed to protect humans would be adequate to protect other species (Copplestone et al., 2004; International Commission on Radiological Protection (ICRP, 1977). However this anthropocentric approach is no longer accepted due to the paucity of information regarding the effects of ionising radiation on non-human biota (Pentreath, 1998; Thompson, 1988), the varying sensitivities of different species and developmental stages to radioactive contaminants (Hagger et al., 2005) and the existence of habitats in which organisms may be exposed to doses above the permissible limits for humans (Copplestone et al., 2001). Assessing the biological impact of ionising radiation on non-human biota has been identified as a necessary approach towards protecting and mitigating the impacts of future radioactive releases on the environment by a number of international directives (e.g., ERICA and PROTECT [Howard et al., 2010; Larsson, 2008]).

The presence of ionising radiation in the environment originates from both natural and anthropogenic sources. Natural sources include cosmic radiation originating from outside the solar system and primordial radionuclides arising from stellar processes (Smith & Beresford, 2005). The majority of anthropogenic radionuclides in the environment are derived from three major sources: nuclear weapons testing, nuclear disasters and permitted discharges from nuclear reprocessing plants (Aarkrog, 2003). The aquatic environment represents an important sink for radionuclides (Avery, 1996), since the majority of deposition of radioactive waste from nuclear facilities is in liquid form and deposition of atmospheric fallout in ocean ecosystems is approximately two-fold higher than in terrestrial systems (Burton, 1975). Radionuclides present in the terrestrial environment may also contribute to radioactivity in aquatic environments via run-off. For ^{137}Cs and ^{90}Sr, the two major man-made contributors to worldwide radiation doses (IAEA, 1995), approximately 2 and 9% of the total land inventories will be transported to aquatic systems respectively via this pathway (Yamagata et al., 1963). However, the bioavailability of radionuclides derived from run-off is often limited by the binding of such radionuclides to particulates and subsequent sedimentation (Aarkorg, 2003). Furthermore, catchment and soil characteristics have been demonstrated to significantly impact the mobility of radionuclides by this pathway (Smith et al., 2004).

Direct disposal of solid radioactive waste into the marine environment was conducted over a 48 year period from 1948 to 1993, leading to dumping of approximately 85 PBq (1×10^{15} Bq) of radioactive material (IAEA, 1999). The majority of dumped waste was low level solid waste deposited in the NE Atlantic and disposal of reactors by the former Soviet Union in the Kara Sea, being 53.4 and 43.3% of total dumped activity respectively (IAEA, 1999). Radiological monitoring of dump sites by a number of organisations revealed negligible impacts on overall radioactive contamination and emphasised the greater influence of atmospheric fallout, although elevated radionuclide levels were observed in the vicinity of some dump sites (i.e., Baxter et al., 1995).

Permitted releases from nuclear reprocessing sites represent a significant source of anthropogenic radionuclides to the world's oceans. For example, the Sellafield nuclear spent fuel reprocessing site located in Cumbria, United Kingdom, generated a liquid radioactive effluent of 6.649×10^5 GBq beta and gamma emitters (excluding tritium) over a four year period from 1995 to 1999 (European Commission, 2001). Such discharges are detectable in most areas of the NE Atlantic and in the Arctic Ocean, representing a significant transfer of radioactive contamination (Kershaw & Baxter, 1995). Major catastrophes such as the explosion at the Chernobyl NPP and the Tōhoku earthquake–tsunami at the Fukushima Dai-ichi NPP led to large scale releases of radioactive material into the environment (Buesseler et al., 2012). Estimates of the overall input of ^{137}Cs to the world's oceans as a consequence of the Chernobyl incident are 15–20 PBq (Aarkrog et al., 2003). Finally the use of radioisotopes in medical, industrial and scientific institutions leads to contamination of the marine environment typically orders of magnitude lower than other major sources (Aarkrog et al., 2003).

Although the need for environmental radioprotection frameworks has long been established, (Pentreath and Woodhead, 1988; Pentreath, 1998) a lack of scientific consensus regarding the doses at which significant biological effects occur (Beresford & Copplestone, 2011) and the disparity between results of laboratory based exposures and field studies (Garnier-Laplace et al., 2013) have precluded a radiological risk assessment for the environment. This provides a contrast with other anthropogenic contaminants wherein protection frameworks and concepts (i.e., the Ecological Risk Assessment concept) are well developed (Bréchignac, 2003). An overview of the effects of ionising radiation on aquatic invertebrates has previously been carried out by Dallas et al., (2012). This paper adopts a phyla-specific approach in order to provide a more detailed analysis of effects, and prioritise research needs for the Crustacea, a group of organisms that have been identified as key models for the development of environmental radioprotection frameworks (ICRP, 2008). Members of the subphylum Crustacea are the dominant components of global aquatic ecosystems and comprise more than 66,000 species (LeBlanc, 2007). These organisms provide an array of commercial and ecological services and are used both directly for human consumption and as a food source for other commercially important species (Benzie, 2009). Due to their ubiquity in aquatic environments and well characterized biology, a marine crustacean of the family Cancridae has been selected as one of the ICRP's reference animals (ICRP, 2008). Reference organisms will be used as a basis to develop environmental radioprotection measures, and are considered ecologically representative of a specified group of plants or animals with biological characteristics amenable to study (ICRP, 2008). To support the development of robust, applicable ecological benchmark values for environmental radioprotection it is necessary to review and identify research needs for radiobiological studies in the selected reference organisms. This paper aims to review the available literature regarding the biological effects of ionising radiation on the crustacean subphylum, draw comparisons across biomarkers and assess any gaps in knowledge in the context of developing dose levels for radioprotection. Emphasis will be placed on studies employing the four biological endpoints as outlined by Copplestone et al., (2008) and Real et al., (2004); mutation, morbidity, reproductive capacity and mortality.

The scope of the literature search was limited to aquatic crustacean species exposed to any form of ionising radiation. The FREDERICA radiation effects database (Available at http://www.frederica-online.org) along with other search engines (Google Scholar, Science Direct and Web of Science) was used as a tool to extract references relating to the four umbrella endpoints selected in this review. The FREDERICA database contains references from a number of European Commission funded projects (i.e., EPIC and FASSET) from 1945 to 2007. All references within this dataset are subject to review based on the adequacy and reproducibility of the study (Copplestone et al., 2008).

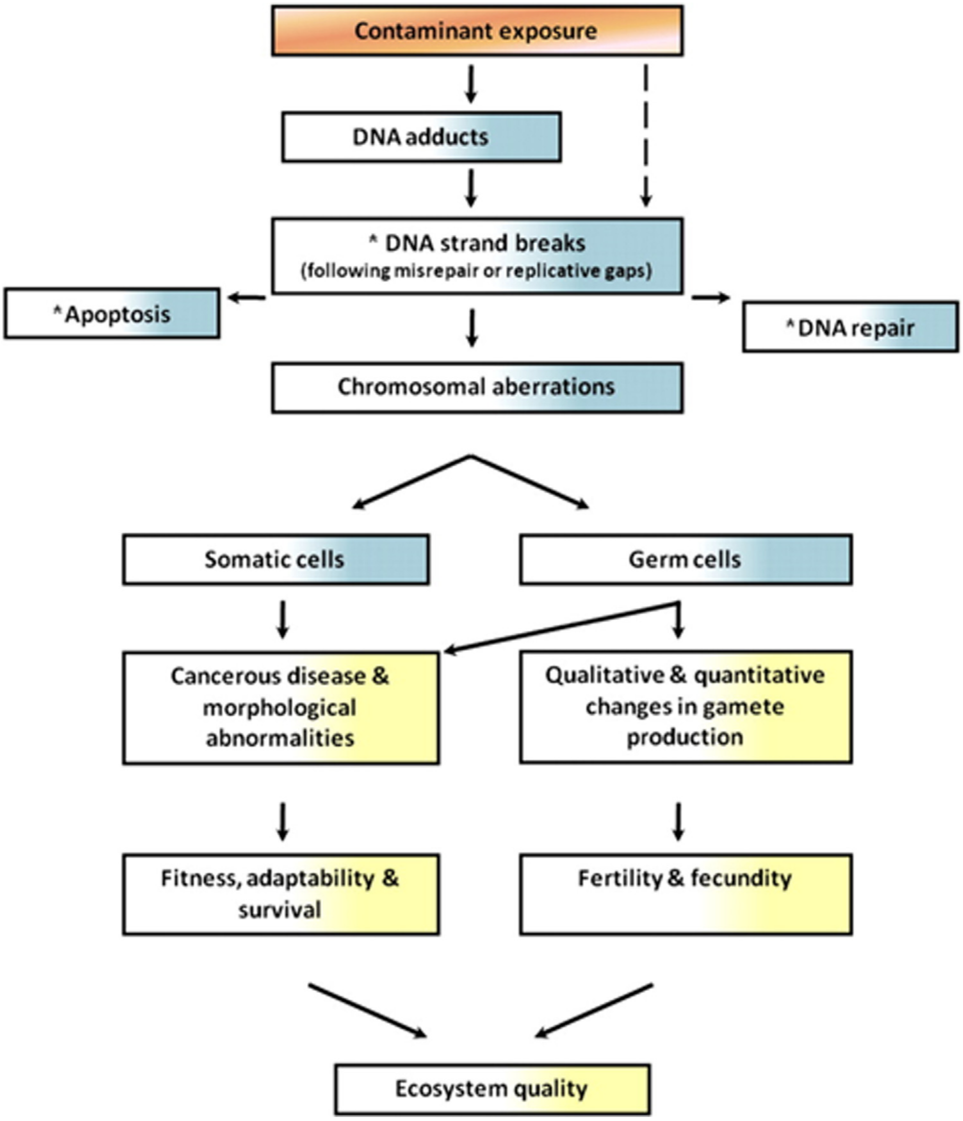

Fig. 1. Illustration of the relationship between contaminant exposure and ecosystem quality. Adapted from Jha (2008). Fig. 1 reproduced with permission from Jha (2008).

2. Radiation-induced mutation in crustaceans

For the purpose of this review, a mutation is defined as "A change in the chromosome or genes of a cell which may affect the structure and development of the resultant offspring" (Copplestone, 2008). Chromosomal and genetic changes have been postulated by a number of authors to have significant ecological implications at higher levels of biological organisation (See Fig. 1 (Anderson and Wild, 1994; Depledge, 1998; Jha, 2008).

Despite evidence suggesting the clastogenic (capacity to cause chromosomal aberrations) and mutagenic potential of ionising radiation observed in a range of organisms including humans (Lucas et al., 1992), fish (Anbumani and Mohankumar, 2012; Kligerman et al., 1975; Pechkurenkov, 1991) and molluscs (AlAmri et al., 2012), there is a paucity of information within the literature regarding the crustacean subphylum. Indeed, the FREDERICA database containing over 30,000 data entries collated from a number of international radiation effects directives contains no data regarding mutation in crustacean species over chronic dose ranges of 0–>10,000 μGy/hr-1 (See Table 1 Copplestone et al., 2008). Similarly, the 2008 ICRP publication introducing the concept of reference animals and plants reported no available data for chromosomal effects in crab species (ICRP, 2008), reiterating the lack of studies in this area.

Field studies have suggested that mutation may be a sensitive endpoint of radiation-induced effects in crustacean species. For example, Florou et al., (2004) assessed chromosomal aberrations in microfauna collected from geothermal spring areas on the island of Ikaria, Greece where maximum dose rates of natural gamma emitters in sediments were 9.6 mGy yr^{-1} (~0.001 mGy/hr^{-1}). These values are substantially elevated above the reported mean of 0.07 mGy yr^{-1} (~0.008 μGy/hr^{-1}) for coastal sediments in Greece (Florou and Kritidis, 1992). An elevated level of cells displaying chromosome aberrations (3.8%) was recorded in populations of the amphipod crustacean *Melita palmata* collected from these areas compared with control sites (1.5–1.7%). The author (Florou et al., 2004) attributed this to increased natural dose rates of gamma and natural alpha emitters, which were also increased above background levels in spring areas (14–26 Bq l^{-1} of ^{222}Rn compared with 1.3–7 Bq l^{-1} in control areas). These dose values fall significantly below proposed environmental protection benchmark values provided by a number of organisations (See Table 2) suggesting induction of significant biological effects below doses that are considered to have no deleterious effects at the population level. However, the biota inhabiting geothermal spring habitats are typically species-poor and subject to multiple stressors including elevated temperatures in winter periods (Flourou et al., 2004)

Table 1
Collation of available chronic radiation effect data and data gaps within the subphylum Crustacea located in the FREDERICA Radiation Effects Database. X = available data - = no data available. Reproduced with permission of Copplestone et al., (2008).

	Dose Rate Range (μGy/hr^{-1})								
	0–50	50–100	100–200	200–400	400–600	600–1000	1000–5000	5000–10,000	>10,000
Morbidity	X	X	–	–	–	X	X	X	–
Mortality	–	–	–	–	–	–	–	–	–
Mutation	–	–	–	–	–	–	–	–	–
Reproductive Capacity	–	–	–	–	–	–	–	–	–

and extremes of pH and chemical toxicants (Duggan et al., 2007). Thus, the observed cytogenetic response in spring biota may have been due to the complex environmental conditions present at the study sites as opposed to the direct effects of ionising radiation. This highlights the inherent difficulties in field radioecology studies (Salbu, 2009) and the importance of quantifying the individual contribution of stressors in environments where abiotic pressures may act synergistically (Dallas et al., 2012). The aforementioned paper represents the only study of natural crustacean populations using mutation as an endpoint. The previously discussed limitations present difficulties in drawing conclusions from this study as observed cytogenetic effects cannot be directly attributed to ionising radiation.

Laboratory studies assessing radiation-induced mutations in crustaceans typically involve acute high doses that are unrepresentative of environmental exposures. Such studies have demonstrated the ability of ionising radiation to induce chromosomal aberrations in crustacean species. Tsytsugina (1998) exposed embryos of two crustacean species, *Idotea baltica* and *Gammarus olivii* to doses of 0.5–5 Gy from a range of radionuclides and chemical mutagens (Lead Acetate and Chlorophene) and scored cells on the presence of chromosomal abnormalities. The mean number of cells with chromosomal aberrations increased concomitant with radiation dose. Furthermore, the author described characteristic types of aberrations produced by the two toxicants which may be used to distinguish between the effects of individual stressors. For example, ionising radiation was shown to elicit chromosomal damage in the form of single and twin fragments, whereas, single and twin bridges were more commonly observed in those embryos exposed to chemical toxicants. The distribution of aberrations between cells was also found to correspond to different statistical distributions dependent on the toxicant, underpinning the potential of this method. However, the karyotype of crustacean species is often reported to be unamenable to cytogenetic study (Salemaa, 1985) due to the typically small size and high diploid numbers of chromosomes (White, 1973). This may preclude application of this method to natural populations.

Recent approaches to assessing radiation-induced genotoxicity in aquatic invertebrates have involved monitoring levels of the expression of genes that are involved in DNA damage repair pathways (AlAmri et al., 2012; Han et al., 2014a; Han et al., 2014b; Won and Lee, 2014). For example, Han et al., (2014b) exposed cultures of the intertidal copepod, *Tigriopus japonicus* to gamma radiation from ^{137}Cs and monitored mRNA expression of three DNA repair genes: *Ku70* (*Xrcc6*), *Ku80* (*Xrcc5*) and *DNA-PK*. These three genes are integral to the non-homologous end joining (NHEJ) DNA repair pathway involved in the detection and repair of radiation-induced double strand breaks (DSBs) (Mahaney et al., 2009). Expression of the three genes was significantly elevated with respect to controls in 200 Gy exposed organisms, suggesting induction of DSBs at these dose levels (Han et al., 2014b). The potential of this approach as a biomarker for genotoxicity in crustacean species was emphasised by Won and Lee (2014) who reported a dose dependent increase in mRNA expression of these genes in another copepod species, *Paracyclopina nana* (See Fig. 2). However, both of these studies used dose levels significantly higher than those encountered in radioactively contaminated environments (except perhaps in the immediate aftermath of a major nuclear accident). Furthermore, in the former study (Han et al., 2014b) gene expression was only monitored at dose levels of 150 and 200 Gy, despite induction of significant biological impacts such as a reduced fecundity in *T. japonicus* at three-fold lower dose levels (50 Gy). Alterations to gene expression patterns and molecular level responses are often reported to be sensitive indicators of contaminant exposure in aquatic invertebrate species (Lee et al., 2006). A recent study supported the previous statement, reporting significant DNA alterations in *Daphnia magna* following exposure to ^{137}Cs doses as low as 0.007 mGy h^{-1} using random amplified polymorphic DNA-polymerase chain reaction (RAPD–PCR) methods (Parisot et al., 2015). Molecular level responses were evident at both lower doses and shorter exposure durations than other endpoints including mortality, morbidity and perturbations to reproduction. Given the sensitivity of molecular endpoints to ionising radiation observed in this publication, it is imperative that a greater number of studies focus on molecular alterations in relation to effects at higher levels of biological organisation to confirm these findings within the crustacean subphylum.

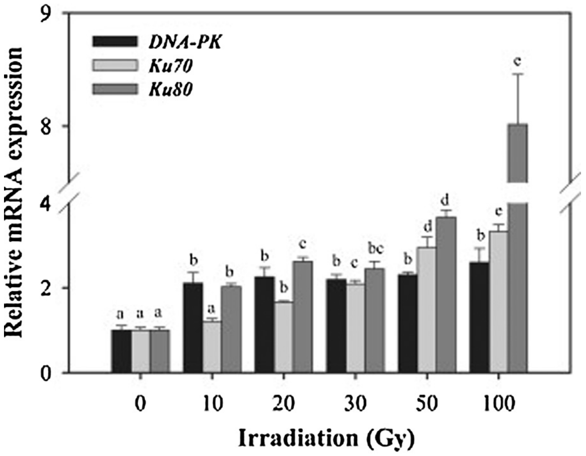

Fig. 2. Dose-dependent increase in mRNA expression of three genes involved in the non-homologous end joining pathway for DNA repair in gamma radiation exposed cultures of the copepod, *Paracyclopina nana*. Fig. 2 reproduced with permission of Won & Lee (2014).

3. Radiation impacts on morbidity in Crustaceans

Morbidity can be broadly defined as “A loss of functional capacities generally manifested as reduced fitness, which may render organisms less competitive and more susceptible to other stressors, thus reducing their life span” (Copplestone et al., 2008). Definition of the term morbidity varies between authors and encompasses a vast number of endpoints including perturbations to growth rates, behavioural alterations and immune system effects (Copplestone et al., 2004). In order to maintain relevance both ecologically and for environmental protection, an endpoint should be amenable to

Table 2

Numerical benchmark values in μGy/hr^{-1} proposed by a number of different organisations and directives for the protection of populations of a range of biota. US DOE = United States Department of Energy. NCRP = National Council on Radiation Protection and Measurements. IAEA = International Atomic Energy Agency. - = No data provided. Adapted from Andersson et al., (2008).

Dose Level (μGy/h^{-1})									
	US DOE (1990)	NCRP (1990)	IAEA (1992)	Environment Canada (2003)	FASSET (2003) Larsson, (2004)	ERICA (2007) Beresford et al. (2007)	ICRP (2008)	UNSCEAR (2008)	PROTECT (2009) Andersson, (2008)
Freshwater Organisms	400	400	400	–	100	10	–	400	10
Algae	–	–	–	100	–	–	–	–	–
Macrophytes	–	–	–	100	–	–	–	–	–
Benthic Invertebrates	–	–	–	200	–	–	–	–	–
Fish	–	–	–	20	–	–	–	–	–
Reference Trout	–	–	–	–	–	–	40–400	–	–
Reference Frog	–	–	–	–	–	–	4–40	–	–
Marine Organisms	400	400	–	–	100	10	–	400	–
Marine Mammals	–	–	–	–	–	–	–	–	–
Deep Ocean Organisms	–	–	1000	–	–	10	–	–	–
Reference Crab	–	–	–	–	–	–	400–4000	–	–
Reference Flatfish	–	–	–	–	–	–	40–400	–	–
Reference Brown Seaweed	–	–	–	–	–	40–400	–	–	
Terrestrial Organisms	–	–	–	100	100	10	–	100	10
Plants	–	–	400	–	–	–	–	–	–
Reference Pine Tree	–	–	–	–	–	–	4–40	–	–
Reference Wild Grass	–	–	–	–	–	–	40–400	–	–
Animals	–	–	40	–	–	–	–	–	–
Invertebrates	–	–	–	200	–	–	–	–	–
Reference Bee	–	–	–	–	–	–	400–4000	–	–
Reference Earthworm	–	–	–	–	–	–	400–4000	–	–
Mammals	–	–	–	100	–	–	–	–	–
Reference Deer	–	–	–	–	–	–	4–40	–	–
Reference Rat	–	–	–	–	–	–	4–40	–	–
Birds	–	–	–	–	–	–	4–40	–	–
Reference Duck	–	–	–	–	–	–	4–40	–	–

Table 3
Summary of morbidity studies in Crustacea. HTO represents Tritiated Water. Acute exposures are defined here as those lasting less than 24 h, with chronic exposures lasting over a period of the organisms life span and greater than 24 h

Species	Dose Rate/Total Dose	Lowest Observed Effect Dose/ Dose Rate (LOEDR)	Radiation Source	Exposure Duration	Exposure Type	Conclusion	Reference
Pollicipes polymerus	7.9, 62.5 nGy/hr^{-1}, 0.625, 6.25 and 62.5 μGy/hr^{-1}	0.000625 mGy/h^{-1}	HTO	32 Days	Chronic	Altered moulting patterns	Abbott & Mix, (1979)
Daphnia magna	0.02, 0.11 and 0.99 mGy/hr^{-1}	0.11 mGy/h^{-1}	^{241}Am	23 Days	Chronic	Reduction in body mass, Increased respiratory demand and Reduction in offspring fitness	Alonzo et al., (2006)
Daphnia magna	0.3, 1.5 and 15 mGy/hr^{-1}	0.3 mGy/h^{-1}	^{241}Am	70 Days	Chronic	Increased oxygen consumption, Reduction in body size and mass across generations	Alonzo et al., (2008a)
Artemia salina	100, 200, 400 and 800 Gy	200 Gy	$^{6^\circ}$Co	~30–220 Minutes	Acute	Decrease in respiration rate	Angelovic & Engel (1968)
Callinectes sapidus	40, 80, 160, 320 and 640 Gy	40 Gy	$^{6^\circ}$Co	~11–175 Minutes	Acute	Behavioural changes; reduction in irritability, catatonic state at high doses	Engel, (1967)
Daphnia magna	0.41, 4.2 and 31 mGy/hr-1	31 mGy/hr^{-1}	^{137}Cs	23 Days	Chronic	Decrease in mass-specific respiration rate, Reduction in offspring fitness	Gilbin et al., (2008)
Nephrops norvegicus	0.5 and 5 Gy	0.5 Gy	$^{6^\circ}$Co	<5 Minutes	Acute	Morphological aberrations; deterioration of cytoplasm and aberrations in cytoplasmic organelles	Mothersill et al., (2001)
Daphnia magna	0.007, 0.07, 0.65, 4.7 and 35.4 mGy/hr^{1}	4.7 mGy/hr^{-1}	^{137}Cs	75 Days	Chronic	Reductions in body length and Von Bertalanffy growth rate	Parisot et al., (2015)
Palaemonetes pugio & *Uca pugnax*	9.75, 19.5, 48.75, 97.5, 195 and 390 Gy	9.1 Gy	$^{6^\circ}$Co	0–20 Minutes	Acute	Alterations to moulting patterns	Rees, (1962)
Pacifastacus leniusculus trowbridgii	2.8, 5.6, 8.4,11.2 and 16.8 Gy	5.6 Gy	X-Ray	1 Minute	Acute	Behavioural changes; detection and avoidance of radiation source	Rodriguez & Kimeldorf (1976)
Macrobrachium rosenbergii	3,30,300 and 3000 mGy	3 mGy	$^{6^\circ}$Co	~0–10 Minutes	Acute	Behavioural changes; alterations to swimming patterns; histological aberrations to the gill	Stalin et al. (2013a)
Macrobrachium rosenbergii	3,30,300 and 3000 mGy	3 mGy	$^{6^\circ}$Co	~0–10 Minutes	Acute	Morphological deformations, Decreased hepatosomatic index	Stalin et al. (2013b)

measurement, specific to the hazard in question and appropriate for extrapolation to higher levels of biological organisation (Ankley et al., 2010; Suter, 1990). The practicality of using morbidity as an endpoint for radiation exposure may therefore be limited due to the lack of specificity and multitude of effects it includes. This is exemplified within the crustacean subphylum, with a diverse array of endpoints (See Table 3 for summary) used to assess morbidity.

3.1. *Radiation-induced impacts on growth & respiration*

Alonzo et al., (2006, 2008a) investigated the effects of chronic internal exposure to the alpha emitting radionuclide, ^{241}Americium, on the growth dynamics of *Daphnia magna*. The authors recorded a significantly lower dry mass and body length of irradiated specimens at doses of ~1.5 mGy/hr^{-1} in first generation organisms (F0), with significant increases in the severity of effects over generations. For example, individuals of the F2 generation displayed a 15% reduction in dry mass at doses of 0.3 mGy/hr^{-1} (Alonzo et al., 2008a). A recent study further underpinned the potential of ionising radiations to perturb growth dynamics in daphnids (Parisot et al., 2015), with reductions of 5 and 13 % in the growth rate of F2 generation daphnids exposed to 4.7 and 35.4 mGy/hr^{-1} of gamma radiation, respectively. Experimental evidence suggests that larger daphnids have enhanced competitive and resource exploitation ability relative to smaller individuals, leading to elevated mortality in those individuals with reduced competition capacity (Kreutzer and Lampert, 1999). The finding that radionuclide exposure may perturb growth dynamics therefore has important implications for natural crustacean population dynamics.

In the previous study (Alonzo et al., 2008a), oxygen consumption of *D. magna* was elevated above controls at all doses, suggesting an increase in metabolic expenditure induced by radiation stress. Exposure of organisms to stressors and adverse conditions may result in reallocation of metabolic energy towards maintenance and lead to reduced energy investment per offspring (Baillieul et al., 2005). This was reflected by a reduced resistance to starvation recorded in neonates derived from 0.02 mGy/hr^{-1} exposed adult daphnids (Alonzo et al., 2006). It is of note that this dose rate falls below the value of ~0.4 mGy/hr^{-1} provided by a number of organisations below which no deleterious population level effects are predicted to occur in aquatic organisms (See Table 2) by an order of magnitude. A recent study (Sarapultseva and Gorski, 2013) further suggested deleterious impacts on neonates relating to metabolic perturbations. Following parental exposure to acute gamma doses of 100 and 1000 mGy from Cobalt-60, a ~20% decrease in the mean life span of non-exposed first generation *D. magna* offspring was demonstrated.

Another study of *Daphnia magna* exposed to chronic gamma irradiation from ^{137}Cs reported contrasting results to the aforementioned study (Alonzo et al., 2008a) of decreased oxygen consumption with increasing dose (Gilbin et al., 2008). *D. magna* receiving gamma dose rates of 31 mGy/hr^{-1} displayed a significantly lower mass-specific respiration rate, compared with dose rates of 0.3, 1.5 and 15 mGy/hr^{-1} all eliciting an increase in respiration rate following Americium-241 (an alpha emitter) exposure in the study of Alonzo et al., (2008a). Whilst the low number of replicates ($n = 6$) recognised by the author in the study of Gilbin et al., (2008) may prevent comparison across studies, this underpins the importance of accounting for differing radiation sources and the corresponding variability in relative biological effectiveness (RBE). The term RBE was coined in 1931 (Failla and Henshaw, 1931) to account for the variability in biological effect observed with dose, dose rate and type of radiation (Valentin, 2003). RBE increases as a function of LET with high linear energy transfer (LET) sources of radiation, e.g., alpha emitters, typically more effective at eliciting biological damage in experimental systems than low LET radiation, i.e., gamma and beta rays reaching a maximum at ~100 keV/μm (Hall and Hei, 2003; UNSCEAR, 1996). This may be used to account for the different responses of *D. magna* in these two studies.

The variability in biological effect relating to the given radiation source is exemplified by a study of morbidity in the goose barnacle, *Pollicipes polymerus*, which recorded altered moulting patterns at extremely low beta doses of 0.62 μGy/hr^{-1} (Abbott and Mix, 1979). The radiation source employed in the previous study was tritiated water (HTO), a radionuclide that is discharged into groundwater systems from nuclear operations (Jaeschke et al., 2011; Jha et al., 2005). Despite the relatively low energy emission of beta particles from HTO (average beta energy of 5.73 ± 0.03 keV (Pillinger et al., 1961), the nature and behaviour of this radiation source within organisms has led to significant concern over the RBE of the radionuclide (Bridges, 2008; Little and Lambert, 2008). It has been demonstrated that HTO may be irreversibly incorporated into organic compounds within organisms (Takeda and Kasida, 1979) and therefore may produce a biological effect disparate with its emission characteristics. In addition, the authors of the aforementioned study on *Pollicipes polymerus* (Abbot and Mix, 1979) stated that calculated doses were exclusive of background radiation which was not quantified. This highlights the importance of robust quantification of received dose in radiobiology studies (Pentreath, 2009).

3.2. The effects of ionising radiation on the behaviour & histopathology of Crustacean species

Ionising radiation has been demonstrated to induce behavioural changes in a number of crustacean species including crabs (Engel, 1967), prawns (Stalin et al., 2013a) and crayfish (Rodriguez and Kimeldorf, 1976). Alterations to behavioural patterns are fundamental in environmental risk assessments since these perturbations may arise as an adaptive mechanism to chronic contaminant exposure and have the potential to alter species–species interactions (Dell'Omo, 2002). The available literature regarding behavioural impacts of radiation involves mostly acute exposures to high doses of radiation (Engel, 1967; Rodriguez and Kimeldorf, 1976), with the magnitude of behavioural changes correlating with dose levels. For example, Engel (1967) assessed the impact of both chronic and acute radiation exposures on the behaviour of the blue crab, *Callinectes sapidus*, a highly aggressive and cannibalistic species (Bushmann, 1999). A reduction in aggressiveness of *Callinectes sapidus* specimens subject to single acute irradiations with $^{6\circ}$Co doses from 40 to 640 Gy was observed, whilst higher doses induced a catatonic state. Continuous exposures to lower doses (0.72, 1.64 & 6.53 Gy/d^{-1}) for 70 days induced cessation of feeding and abnormal behavioural patterns deviating from the normal pugnacious nature of *C. sapidus*, with the extent of behavioural effects relating to dose. Whilst the received dose remains significantly higher than estimates of the highest external doses in freshwater systems immediately after the Chernobyl accident ([4.2–8.3 mGy/hr^{-1} from bottom sediments] Kryshev et al., 2005), the finding that prolonged exposures may perturb behavioural patterns has implications for contaminated areas where radiation levels remain elevated over long time scales. Furthermore, limited data suggests induction of behavioural effects at lower, environmentally relevant doses. Stalin et al., (2013a) demonstrated behavioural changes including alterations to swimming patterns in the giant freshwater prawn, *Macrobrachium rosenbergii* at acute gamma doses of 3 mGy.

Few studies have considered the impacts of ionising radiation on morphological and histological parameters in crustaceans. Stalin et al., (2013a,b) demonstrated induction of histological and morphological aberrations including swollen and necrotic lamellae in the gill, deformations of the uropod, and discolouration of the abdomen in *M. rosenbergii* over a dose range of 3–3000 mGy (Stalin et al., 2013a), with the magnitude of effects relating to dose. Iwasaki (1973) adopted a histological approach to assess gamma radiation-induced effects in oogonia and oocytes of the brine shrimp, *Artemia salina*. A dose-dependent increase in cellular deformations and the number of pyknotic cells (cell degradation characterised by chromatin condensation) was recorded over a high dose range of 250–3000 Gy from Cobalt-60. Furthermore, Mothersill et al., (2001) recorded perturbations to cytoplasmic organelles in hematopoietic cultures of *Nephrops norvegicus* at gamma doses of 0.5 Gy. Deformations included abnormal mitochondrial-rough endoplasmic reticulum complexes at 0.5 Gy, progressing to complete disintegration of the cellular cytoplasm at doses of 5 Gy. Structural perturbations to the gill lamellae of crustaceans have been recorded in response to a number of toxicants (Li et al., 2007; Saravana Bhavan and Geraldine, 2000) and may ultimately impair gill functioning (Tamse et al., 1995) leading to asphyxia. Future studies should consider histological impacts on the crustacean gill using chronic, environmentally relevant radiation doses in order to corroborate this finding. A decrease in the hepatosomatic index of *M. rosenbergii* was also observed as a consequence of radiation exposure (Stalin et al., 2013b) which may provide further evidence that radiation elicits alterations to energy budgets since changes to the HSI may reflect mobilization and utilization of energy reserves (Sánchez-Paz et al., 2007).

Behavioural analysis of crustacean species exposed to ionising radiation has relied largely upon anecdotal visual observations over a defined time period (Stalin et al., 2013a). This approach is subject to a number of limitations including a lack of test standards (Kane et al., 2004), a low sensitivity comparable with video-based behavioural analysers and the potential for individual bias. Furthermore, the available studies have employed acute radiation exposures which may induce different behavioural effects to equivalent doses delivered over longer time scales (Solomon et al., 2009). Future studies should couple chronic, environmentally relevant exposure durations with a high-throughput behavioural tracking system. Such systems minimise bias by providing sensitive, reliable recordings of small animal behaviour under controlled conditions.

4. The effect of ionising radiation on reproduction in Crustaceans

Reproductive endpoints are frequently the subject of ecotoxicological and environmental risk assessments studies since perturbations to reproduction may impact upon the long-term survival of a species and hence alter ecosystem dynamics (Anderson and Wild., 1994; Dallas et al., 2012). A large number of publications have focused on radiation-induced effects on reproductive parameters in aquatic invertebrates, with the reported dose level at which significant effects occur varying by at least two orders of magnitude (Harrison and Anderson, 1996). This remarkable variability is exemplified within the crustacean subphylum; for example Alonzo et al., (2008a,b) recorded a delayed brood production in *D. magna* exposed to 15 mGy/hr^{-1} over a 23 day period (total dose of 0.345 Gy), however 10 Gy was needed to elicit a delay in the reproduction of the marine copepod, *Paracyclopina nana* (Won and Lee, 2014). Differences in the exposure duration, specific radionuclide and endpoint employed preclude development of a generalised 'dose limit' for reproductive effects in crustacean species. One of the priority areas for future research in radioecology is assessing the consequences of multigenerational radiation exposure. This was identified in the research agenda of the Strategy for Allied Radioecology (STAR) group (Hinton et al., 2013) on the basis that exposures across generations have long been a focus in human radiobiology and epidemiology studies (Dubrova et al., 2000; Koturbash et al., 2006; Nomura, 1988), but comparatively ignored in non-human biota. Radiation-induced perturbations to reproductive parameters may be particularly relevant in multigenerational exposure scenarios, since such perturbations may alter population dynamics and the subsequent ability of offspring to adapt to environmental stressors (Alonzo et al., 2008b; Lynch, 1989, 1992).

The available literature within the crustacean subphylum suggests the presence of effects over multiple generations (Alonzo et al., 2008a; Plaire et al., 2013; Massarin et al., 2010; Parisot et al., 2015; Sarapultseva and Gorski, 2013). Alonzo et al., (2008a) and Massarin et al., (2010) recorded an increase in the magnitude of deleterious effects across generations in *Daphnia magna* exposed to chronic alpha irradiation and chronic waterborne uranium exposure, respectively, with severe impacts to fitness and reproduction in individuals of the F_2 generation. In contrast, the multigenerational study of Parisot et al., (2015) reported a degree of recovery in F1 generation daphnids and a reduced radiosensitivity relative to the parental generation across both lethal and sub-lethal endpoints (mortality and fecundity, respectively). Differential radiosensitivity between developmental life stages has been widely recorded within the crustacean subphylum, demonstrated in copepods (Bardill et al., 1977) and *Artemia* species (Metalli et al., 1961). The authors (Parisot et al., 2015) hypothesised that a cumulative radiation dose may be necessary to elicit compensatory mechanisms such as DNA repair, accounting for the differential radiosensitivity between generations. Studies of radionuclide exposed daphnids using RAPD–PCR methods have indicated transmission of DNA damage from adult female daphnids to progeny across generations (Parisot et al., 2015; Plaire et al., 2013). This may be mediated by an epigenetic mechanism, as has been proposed for the transmission of effects in *D. magna* exposed to a range of chemical toxicants (Vandegehuchte et al., 2010) causing alterations to gene expression across generations. Further molecular studies are necessary to elucidate this mechanism. Given the increase in magnitude of reprotoxic and the associated deleterious effects on population dynamics (Alonzo et al., 2008a, 2008b) observed over generations, it is imperative that future studies continue to adopt a multigenerational approach as studies derived from single generation exposures may underestimate risk (Massarin et al., 2010).

Studies within the crustacean subphylum are heavily biased toward female reproductive success, with typical endpoints including production of new eggs (Won and Lee, 2014), hatchability of eggs (Iwasaki, 1964; Sellars et al., 2005) egg mass (Alonzo et al., 2006, 2008a) and time of hatching (Gilbin et al., 2008). Comparatively, radiation-induced effects on male fertility have been ignored. To the author's knowledge no study has directly recorded the impacts of ionising radiation on male fertility. Sperm are considered sensitive to the influence of xenobiotic stressors including ionising radiation (Fischbein et al., 1997; Lewis and Ford, 2012; Marques et al., 2014). This is attributed to their lack of inherent defence systems such as antioxidant enzymes and DNA repair comparable with other biological systems (Trapp et al., 2014). A number of studies have confirmed the sensitivity of sperm to anthropogenic radionuclides. Following the Chernobyl catastrophe an elevated incidence of sperm morphological abnormalities and perturbations to spermatogenesis was observed in liquidators exposed to doses of up to 0.25 Gy (Cheburakov and Cheburakova, 1992; Fischbein et al., 1997). Furthermore laboratory studies of plaice, *Pleuronectes platessa*, have demonstrated that chronic exposures to environmentally relevant low doses of gamma radiation (0.24 mGy/hr^{-1}) are sufficient to cause a significant reduction in sperm number in these organisms (Knowles, 1999). Experimental evidence in aquatic invertebrates has suggested that reductions in sperm numbers may have subsequent effects at higher levels of biological organisation. This is exemplified by Dunn et al., (2006), who recorded a 55% reduction in the size of freshwater amphipod (*Gammarus duebeni*) broods after mating with males displaying a sperm count reduction of 56% (Lewis and Ford, 2012). Coupling the ecological relevance of perturbations to sperm parameters with the known sensitivity of sperm, it is imperative that future studies within the Crustacea include these endpoints within radiobiological studies.

5. Radiation-induced mortality in Crustaceans

Despite the recent trend towards studies using chronic exposures of sub-lethal doses, the available literature of radiation effects in crustaceans remains dominated by mortality studies. This data is often used to calculate lethal dose (LD_{50}) values (Dallas et al., 2012) in order to derive hierarchies of radiosensitivity across taxonomic groups (Blaylock et al., 1996; Harrison and Anderson, 1996). LD_{50} values are traditionally used in ecotoxicological studies to determine the ecological risk to species (Stark et al., 2004) and have also been employed in order to determine no observed effect concentration (NOEC) values (Garnier-Laplace et al., 2006) to inform radioprotection and regulatory efforts. However, many studies have highlighted the greater sensitivity and ecological relevance of reproductive endpoints in radiation studies compared with measurements of adult mortality (Garnier-Laplace et al., 2006; Jones et al., 2003; UNSCEAR, 2008). This was further emphasised by Alonzo et al., (2008b) who found that an increase in individual mortality had a reduced effect on *D. magna* population growth relative to perturbations to two reproductive biomarkers (See Fig. 3). In contrast, Stark et al., (2004) recorded that within some species stress-induced individual mortality had a greater effect on intrinsic population increase than perturbations to reproductive capacity. Mortality has the potential to alter the age distribution, death rate and density of a population (UNSCEAR, 2008). Furthermore, the derivation of LD_{50} values is necessary to elucidate a given species sensitivity to radiation and to determine appropriate dose levels to employ in laboratory radiobiology studies. This serves to reiterate

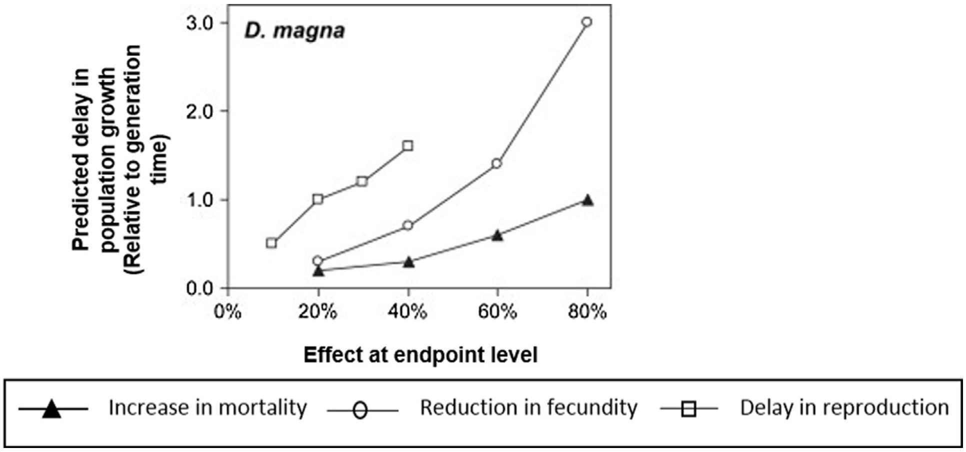

Fig. 3. Predicted delay in population growth relative to generation time in *Daphnia magna* populations exposed to alpha radiation determined using single generation models. The effects of increased mortality, fecundity reductions and delays in reproductive processes at the endpoint level are modelled. Reproduced with permission of Alonzo et al., (2008b).

the importance of including a number of endpoints in radioecology studies and that in some cases derivation of lethal dose data remains relevant.

Within the crustacean subphylum, the dose at which mortality occurs displays remarkable variability (Dallas et al., 2012). Recent work using the harpacticoid copepod *Tigriopus japonicus* demonstrated tolerance of external gamma radiation doses of up to 600 Gy, with mortality only occurring 5 days after cessation of exposure (Han et al., 2014). This is within the same order of magnitude as some bacteria and protozoan species, groups considered amongst the most radioresistant organisms (Copplestone et al., 2001). Furthermore, upon irradiation of dry egg masses, Iwasaki et al., (1971) demonstrated extreme radioresistance in *Artemia salina* nauplii of up to 2780 Gy one day after hatching. However, *Artemia* cysts display remarkable resistance to a range of stressors (MacRae, 2003) attributed to their greatly reduced metabolic and developmental activity prior to hatching and therefore are not considered representative of other crustacean species. Conversely, Rees (1962) reported a 30 day LD_{50} of ~15 Gy in the grass shrimp, *Palaemonetes pugio* which is within the upper bounds of radiosensitivity of some mammalian species (Blaylock et al., 1996). There are many problems associated with using lethal dose data to compare radiosensitivity across organisms. For example, there is a lack of standardisation of the duration used to calculate lethal dose data varying from 4 days (Han et al., 2014) to 40 days (Engel, 1973) which may greatly influence the final value. For chemical toxicants, this parameter has been standardised in published guidelines for tests using *Daphnia* species (OECD, 2004), enabling direct comparisons of LD_{50} values across stressors. Radiobiological studies would benefit from adopting a similar approach in order to aid comparative ability.

Comparatively, the effects of chronic radiation doses on mortality in crustaceans have been underrepresented. Marshall (1966) exposed 25 populations of *Daphnia pulex* to external gamma radiation over a 55 week period for 18.5 h a day with doses ranging from 0 to ~5.1 Gy/d^{-1}. At the three highest dose levels (~5.1 Gy/d^{-1}, ~4.8 Gy/d^{-1} and ~4.36 Gy/d^{-1}) populations crashed and became extinct, which the author attributed to an increase in individual death rate approaching the upper limit of the sustainable birth rate. Other monitored parameters such as the% of aborted eggs and embryos were shown to increase at dose levels below those leading to extinction, reiterating the greater sensitivity of reproductive endpoints comparable to mortality. Parisot et al., (2015) corroborated these findings, reporting a slight but non-statistically significant increase in mortality in ^{137}Cs exposed *D. magna* at a dose rate of 35.4 mGy/h^{-1}, with sub-lethal impacts occurring at much lower dose rates of 0.007 mGy h^{-1}. Engel (1967) exposed blue crabs, *Callinectes sapidus*, to acute doses (maxium of 180 min exposure) of gamma radiation from $^{6^\circ}$Co over a total dose range of 40–640 Gy at a dose rate of 219 Gy/hr^{-1}. The author also continually exposed *C. sapidus* to dose rates of 0.032, 0.073 and 0.29 Gy/hr^{-1} over a 70 day period. Following acute exposure a 30-day LD_{50} of 510 Gy was recorded. In contrast, crabs subjected to a total accumulated dose of ~460 Gy at the dose rate of 0.29 Gy/h^{-1} over a 70 day period displayed 100% mortality. Although the difference in total dose precludes useful comparison, the greater sensitivity of *C. sapidus* following continuous exposure underpins the importance of the exposure duration in determining biological impact in radiobiology studies. Dose rate has been reported to be an important factor in determining biological effects across a range of organisms including insects (Russell et al., 1958), humans (Elmore et al., 2006) and rodents (Russell et al., 1959). For example, Shimada et al., (2005) demonstrated a dose rate dependency of transgenerational mutation frequencies in spermatogonial stem cells of Medaka, *Oryzias latipes*. The authors exposed male medaka to an 80 TBq^{137} Cs source at dose rates of 3 Gy/min and 9500 Gy/min, and recorded a lower mutation frequency at each total dose (1.9, 3.2 and 4.75 Gy) in the 3 Gy/min group.

6. Conclusions

Despite numerous international directives and decades of research into the biological effects of radiation, significant gaps in our knowledge still remain. Although current research trends indicate an increase in the number of publications using environmentally relevant radiation sources and durations (Dallas et al., 2012), a significant disparity between the number of acute and chronic studies persists. This is exemplified within the FREDERICA radiation effects database. Within this database, 64% of the data points were obtained following acute radiation exposures, with 36% following chronic exposures. Furthermore, the available chronic data is heavily biased towards fish, mammals and terrestrial plants with a scarcity of data evident in the crustacean subphylum (See Table 1 (Copplestone et al., 2008). Another major limitation is the discrepancy between the available data for laboratory toxicity tests comparable with field studies. The majority of field data is heavily biased towards small mammals (Baker et al., 1996; Beresford et al., 2008; Chesser et al., 2000), fish (Dallas et al., 1998; Jonsson et al., 1999; Sugg et al., 1996 Jonsson et al., 1999; Sugg et al., 1996), plants (Kovalchuk et al., 1998, 2000; Syomov et al., 1992) and

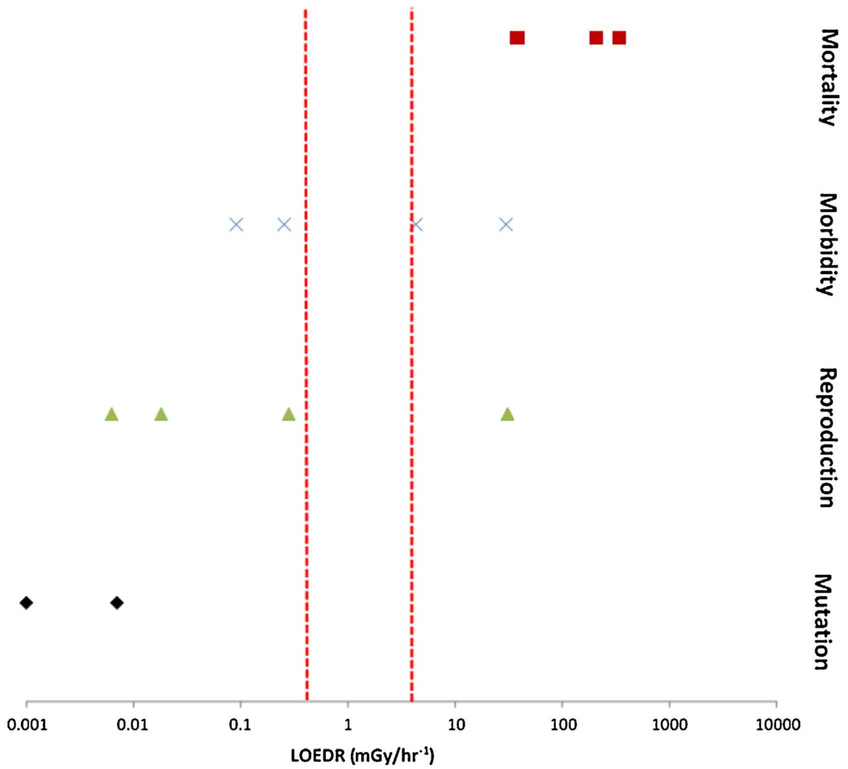

Fig. 4. Summation of the available chronic effect data within the crustacean subphylum across four endpoints; mortality, morbidity, reproduction and mutation. The lowest observed effect dose rate (mGy/h^{-1}) is used on a logarithmic scale. The band of dose rates selected by the ICRP (2008) DCRL for the reference crab is indicated by.

birds (Bonisoli-Alquati et al., 2010; Galván et al., 2014; Hermosell et al., 2013). Comparatively, the majority of field studies regarding crustacean communities exposed to radionuclides are focused on bioaccumulation of radioactive materials (Marzano et al., 2000) relating to trophic transfer, or calculating estimates of received doses (Murphy et al., 2011; Batlle et al., 2014).

A summary of the available chronic effect data and the corresponding lowest observed effect dose rate (LOEDR) in crustacean species is shown displayed in Fig. 4. From the limited available data, a tentative hierarchy of radiosensitivity in the four endpoints can be derived as follows: mutation > reproduction > morbidity > mortality. Whilst it must be reiterated that this is based on extremely limited data (two data points for mutation, see Fig. 4), this may challenge the assumption that reproduction is the most sensitive endpoint of radiation exposure in non-human biota (UNSCEAR, 2008). Responses at the molecular level, i.e., alterations to gene expression, are frequently recorded to be sensitive indicators of toxicant exposure across a range of organisms (See Section 2). Although recent crustacean radiobiology studies have demonstrated a shift towards use of molecular level endpoints (See Section 2 (Han et al., 2014b; Parisot et al., 2015; Won and Lee, 2014)), the use of ‘ecotoxicogenomics’ (the integration of genomic techniques in response to environmental toxicant exposure (Iguchi et al., 2007)) has been a focus of studies of other toxicants IE endocrine disruptors for almost a decade (Seo et al., 2006). The observed sensitivity of mutation as an endpoint observed in this paper highlights the need to exploit the advent of cheaper and more accessible molecular analyses in order to validate the usefulness of mutation as an endpoint and evaluate the potential of these techniques as tools in environmental radioprotection and radioecology. It is important to note that establishing linkages between gene expression analyses and endpoints of higher levels of biological organisation such as reproduction, survival and development remains a significant challenge in applying ecotoxicogenomics to ecological risk assessments (Miracle and Ankley, 2005). Furthermore, transcriptional changes do not necessarily elicit a biological effect within a given organism (Schirmer et al., 2010). Whilst this approach offers huge potential, until clear experimental links can be drawn between alterations to gene expression patterns and effects at higher levels of biological organisation, monitoring endpoints with clear ecological implications such as reproduction, development and growth remains important.

In conclusion, this review has summarized the available historic and current literature pertaining to radiation-induced effects in an ecologically relevant and model subphylum. Such effects are observed over a wide range of dose rates and exposure sources, and could conceivably have ecological consequences for biota chronically exposed to elevated levels of radionuclides. At present however there is limited population level data for aquatic organisms inhabiting chronically contaminated areas. Indeed, a study of the abundance and diversity of macroinvertebrate communities at eight Chernobyl affected lakes (Murphy et al., 2011) found no evidence of radionuclide contamination impacting the ecological status of the water body, and recorded the highest taxon richness at the most contaminated lake (estimated total external doses of 30.7 μGy/hr). Clearly, further studies at higher levels of biological organisation are necessary to elucidate the potential ecological consequences of the effects outlined in this review. Finally, this review has highlighted the persistent paucity of data across commonly used endpoints in the crustacean subphylum and identified key gaps in the literature to enhance research within the field. These data gaps must be addressed in order to enhance the efficacy of the subphylum Crustacea as a reference point for the optimisation and development of environmental radioprotection frameworks.

Conflict of interest

The authors declare no conflict of interest.

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