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Radionuclide transfer through coastal food webs in darker and warmer waters

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Abstract

Global climate change, leading to warming and increased precipitation in northern latitudes, is expected to increase the transfer of organic matter from soils to coastal waters. This inflow does not only bring particulate organic matter (POM) but also brown-coloured dissolved organic carbon (DOC), which darkens the water. Water darkening alters coastal food web structure and dynamics by affecting the system from bottom up, suppressing benthic primary production while favouring bacterial production and potentially also from the top down by hindering visual predators. Global climate warming further changes coastal food webs from the top down by increasing consumer metabolic rates, especially in large-bodied fish species, which increases costs for maintenance, consumption rates and thus body growth. This can lead to decreased fish biomass production and a shift towards dominance of smaller individuals. While the ecological consequences of warming and darkening are increasingly studied, their effects on contaminant transfer remain poorly understood. One likely outcome of water darkening is a shift from benthic to pelagic primary production, pushing omnivorous fish to rely more on pelagic resources, such as zooplankton. Such shifts in habitat use and species interactions are critical for contaminant transfer, as radionuclides such as ^{137}Cs bioaccumulate mainly through diet. If fish switch from benthic prey with higher ^{137}Cs concentration to zooplankton with lower contaminant levels, they may accumulate less radionuclides. In this essay, I review causes and consequences of warming and darkening of waters and discuss how coastal food web responses to these drivers may be key to predict radiocesium transfer and bioaccumulation, and thus important to risk assessment.

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Abbreviations

| | |
|------|--|
| ADOM | Allochthonous dissolved organic matter |
| AE | Assimilation efficiency |
| cDOM | Coloured dissolved organic matter |
| CF | Concentration factor |
| DOC | Dissolved organic carbon |
| DOM | Dissolved organic matter |
| MTE | Metabolic theory of ecology |
| OM | Organic matter |
| tDOM | Terrestrial dissolved organic matter |
| TF | Transfer factor |
| TSR | Temperature-size-rule |

1. Introduction

Increased CO₂ levels in the atmosphere have resulted in a rise in average air temperature, increased sea surface temperatures and altering of coastal ecosystems globally (Varela et al. 2023). The Baltic Sea, due to its enclosed and shallow morphology and northern location, is warming at a faster rate (0.4–0.6°C per decade) than other similar sea areas globally (HELCOM 2023). In addition to rising mean sea surface temperatures, global change is expected to further increase precipitation in high latitudes (30°N–85°N). In Fennoscandia, annual precipitation has already increased by 10–40 % during the 20th century, in contrast to southern Europe where precipitation instead has decreased by as much as 20 % during the same time (Dore, 2005). Increased precipitation results in increased river runoffs, and thus more freshwater transferring nutrients and terrestrial organic matter (t-OM) from land to the sea (Wikner & Andersson, 2012). In addition to excess nutrients and dissolved organic carbon (DOC) causing eutrophication and darkening of waters, river runoff can also transport contaminants, including radionuclides, to coastal waters during periods of high precipitation (Hayashi *et al.* 2022; but see Fuji *et al.* 2018). However, there is limited understanding of contaminant behaviour and transfer under climate change, especially with respect to coastal waters becoming warmer and darker (Larsen *et al.* 2011). These knowledge gaps make it challenging to predict contaminant transfer and bioaccumulation in coastal ecosystems, increasing the likelihood of environmental risks (Hatje *et al.* 2022).

For all organisms, temperature and therefore warming, influences individual physiology and thus body growth and size. In ectothermic organisms, which make up over 99% of all species on Earth, body temperature is determined by the environment, leading to a direct link between temperature and body size (Block 2024; Forster et al. 2012). The metabolic theory of ecology (MTE) outlines how temperature affects metabolic rate, and consequently resource uptake and allocation, independently of body size (Brown *et al.* 2004). However, empirical and theoretical studies have shown that temperature's effects are size-specific, both at the individual, population, and community-level (Lindmark *et al.* 2022). Warming has been shown to shift fish and zooplankton population and community structure towards dominance of smaller individuals (Uszko *et al.* 2022; Van Dorst *et al.* 2019), which may affect overall food web dynamics (Lindmark *et al.* 2018, 2019).

Looking at warming and natural variation in temperature, Huss *et al.* (2019) and Van Dorst *et al.* (2019) have shown how warming is likely to more positively affect body growth of young than old and large fish. This is in line with the temperature-size-rule (TSR) according to which ectotherms in warmer environments grow at a faster rate but reach smaller asymptotic size (Forster *et al.* 2012; Angilletta *et al.* 2004). Accordingly, there are examples of warming increasing body growth in small individuals making them bigger at younger age (Huss *et al.* 2019), but leading to smaller adult size and therefore earlier maturation and gonad development (Baudron *et al.* 2014; Niu *et al.* 2023 *but see* Lindmark *et al.* 2023). In addition to fish size and population biomass, warming can have a direct positive effect on aquatic primary production if they have sufficient nutrients and light available (Häder *et al.* 2014; Bernhardt *et al.* 2018). However, warming-induced increases in phytoplankton growth rates is not always expected to compensate for the increased metabolic rates and foraging of larger-bodied herbivores (in this case zooplankton) at higher temperatures, restricting phytoplankton standing stock biomass (O'Connor 2009). Still a recent study by Mooney *et al.* (2025) found a positive relationship between lake phytoplankton biomass and temperature, suggesting that increased phytoplankton growth rates were not offset by increased grazing rates at high temperatures. However, it is important to note that in the study by O'Connor (2009), zooplankton was not predated and the study system consisted of only two trophic levels, whereas in Mooney *et al.* (2025) the system consisted of three trophic levels, highlighting the role of food chain length in warming-induced effects.

Terrestrial dissolved organic matter (t-DOM), often referred to in the literature as allochthonous dissolved organic matter (ADOM) because it originates from external sources (Figuerola *et al.* 2016), includes coloured dissolved organic matter (cDOM). This is one of the major factors causing browning and darkening of waters in lakes and coastal areas that receive high inflows of freshwater from rivers and streams (Vasconcelos *et al.* 2016; Figuerola *et al.* 2016, see also Opdal *et al.* 2023 for effects in waters far from the shore). Browning is a term generally used for freshwater systems, and darkening is the equivalent process in coastal waters, both being caused by cDOM and with direct and indirect effects on aquatic ecosystems. For example, darker waters can directly affect fish behaviour, especially with respect to foraging rates of visual predators (Weidel *et al.* 2017), and indirectly their body growth, biomass production, as well as energy flow between organisms at different trophic levels (van Dorst *et al.* 2019). Darkening of waters decreases the amount of light that reaches the benthic primary producers. Thus, water darkening reduces benthic primary production, lowering the ecosystem's total primary productivity and the proportion of total production contributed by benthic relative to pelagic primary producers living in upper layers of the water column where light is sufficient (Ask *et al.* 2016; Karlsson *et al.* 2009). At high levels, increased allochthonous carbon loading have also been shown to suppress pelagic

phytoplankton biomass production, while favouring growth of pelagic heterotrophic bacteria (Wikner & Andersson *et al.* 2012; Ask *et al.* 2009). With the microbial pathway, that contain additional trophic levels, becoming increasingly more important with DOM loading, energy will flow through more trophic levels before reaching fish. This means more energy is lost and the energy transfer efficiency lower, which results in a decrease in biomass production in higher trophic levels (Berglund *et al.* 2007; van Dorst *et al.* 2019).

Anthropogenic pollution of persistent contaminants, such as heavy metals and radionuclides, is a serious threat to environmental well-being due to their toxicity and persistence in the environment that make them bioaccumulate in organisms and in some cases biomagnify in food chains (Ali and Khan 2019). Radioactivity in the Baltic Sea is possibly higher than in other similar water bodies around the world due to its unique morphology, slow water exchange and rapid sedimentation (HELCOM 2013). After contamination from the Chernobyl fallout in 1986, especially ^{137}Cs concentrations are higher in the Baltic Sea than other places in the world (Ikäheimonen *et al.* 2009). Studies of ^{137}Cs bioaccumulation in the Baltic Sea offers valuable information on radionuclide bioaccumulation due to ^{137}Cs long physical half-life (30.17 years), naturally low background levels and tendency to bioaccumulate to fish muscle tissues without metabolising (Sundbom *et al.* 2003). Previous studies have shown that radionuclides and especially ^{137}Cs bioaccumulation to tissues increases with fish size, trophic level and vary with feeding habits (Rowan *et al.* 1998) and temperature (Nakahara *et al.* 1977). In addition, increases in particulate organic matter input has been also shown to significantly impact transfer and export of ^{137}Cs from soils to marine ecosystems, thereby increasing radionuclide concentrations in the coastal areas (Naulier *et al.* 2017).

With increased river runoffs (Wikner & Andersson, 2012) affecting both water darkness and primary production (Ask *et al.* 2009; Karlsson *et al.* 2009), there is a need for a better understanding of how increasing organic matter input to coastal ecosystems is affecting radionuclide bioaccumulation and transfer, both alone and in combination with warming. Along with the accelerated warming of sea surface waters, it is important to understand other processes affected by environmental change when evaluating and modelling radionuclides transfer through aquatic food webs. The aim of this essay is to review how coastal food web responses to the combination of warming and darkening may influence radionuclide bioaccumulation and biomagnification, through both direct pathways and indirect pathways mediated by species interactions.

2. Warming and darkening of coastal waters

2.1 Coloured terrestrial organic matter causes darkening of waters

2.1.1 Primary production in coastal ecosystems

Shallow coastal areas are ecologically important ecosystems that support high biodiversity and serve as critical habitats for most marine organisms during some stage of their life cycle (Henseler et al. 2019). In addition, coastal areas are highly productive (Pauly and Christensen 1995), and their total primary production is driven by both pelagic and benthic primary producers (Ask *et al.* 2016). In the pelagic zone, referring to the upper water column in the open area of water bodies, basal producers include pelagic phytoplankton capable of photosynthesis, along with heterotrophic bacteria. Both groups can act as energy mobilizers, acting as a link between the chemical environment and higher trophic levels, regulating carbon flows and therefore energy transfer (Andersson *et al.* 2018). For pelagic food web dynamics, also the community structure of these basal producers is important. Herbivorous zooplankton typically favours feeding on larger phytoplankton, and in turn zooplankton serves as a resource to larger animals at higher trophic levels. In contrast, smaller sized phytoplankton often boosts the microbial food web by releasing DOM that promoted bacteria and the protozoa that graze on them (Legendre & Rassoulzadegan 1995). In pelagic habitats, where the light climate is generally favourable but nutrient concentrations are typically low, phytoplankton growth is often limited by nutrient availability, particularly nitrogen, both globally in marine and in the Baltic Sea (Howarth 1988; HELCOM 2021).

Benthic primary producers consist of a large variety of organisms such as macro- and microalgae and aquatic plants. Macroalgae and seagrasses are often epiphytes growing on rocks and the surfaces of other algae (Borowitzka et al. 2006) and can be seen with the naked eye. In contrast, microalgae attach to different substrates such as hard rocks and soft sediments and can only be distinguished with a microscope (Allan *et al.* 2021; Ask *et al.* 2016). Due to living close to the sea floor,

benthic primary producers have access to nutrient-rich sediments but are often light-limited due to shading and turbidity caused by phytoplankton, as well as the darkening of the upper water column caused by coloured dissolved organic matter (cDOM) (Karlsson *et al.* 2009; Harvey *et al.* 2015). Consequently, in deeper areas with strong light limitation, pelagic primary production is responsible for almost the entire ecosystem's total primary production (Sand-Jensen & Borum 1991). In contrast, in clear and shallow waters, primary production is dominated by benthic algae (Vadeboncoeur *et al.* 2003) and therefore the proportion of benthic primary production of total primary production can be significant in clear waters (Ask *et al.* 2009). For example, in the Baltic Sea, benthic primary production contributes up to 17% to the total annual primary production in estuaries and up to 31 % in entire bay areas (Ask *et al.* 2016).

Coastal habitats are typically rich in both organic and inorganic particulate and dissolved matter. Some of this material originates from land, including terrestrially derived dissolved organic carbon (DOC) (Opdal *et al.* 2023; Frigstad *et al.* 2023), along with other substances derived from terrestrial plant material that are transformed in soils through interactions with minerals and microorganisms (Solomon *et al.* 2015). Besides dissolved substances, t-OM also contains particulate organic matter (POM), of which some aggregate and sink to the bottom sediments due to its weight (Solomon *et al.* 2015) and thus serve as a resource for benthic organisms (Bartels *et al.* 2018). These organic substances are carried by freshwater inputs to estuaries, and can especially in marine upwelling areas, result in murky nutrient-rich waters (Häder *et al.* 2014). For example, Frigstad *et al.* (2023) showed that a 23–85% increase in riverine discharge resulted in a 40–78% increase in suspended organic particulate material in coastal waters, contributing to reduced water clarity. Water darkening, also referred to as browning or brownification (mainly in freshwaters), describes the darkening of water colour caused by dissolved organic carbon (DOC) and suspended particles that absorb sunlight and thereby reduce the light available for photosynthesis (Kritzberg *et al.* 2020; Harvey *et al.* 2015). Darkening of coastal waters is recognized as an environmental concern, with yet poorly understood ecological impacts on coastal ecosystems (Bartels *et al.* 2018; Opdal *et al.* 2023).

2.1.2 Effects of water darkening on benthic and pelagic habitats

Water darkening directly affects both benthic and pelagic habitats. In benthic environments, reduced light availability can negatively affect benthic primary producers, leading to decreased benthic biomass production (Ask *et al.* 2009). This reduction in benthic biomass production can propagate up through food webs, ultimately affecting higher trophic levels such as fish that rely on benthic invertebrates as a food resource (Karlsson *et al.* 2009). As light availability at the

bottom declines, the benthic share of total primary production declines relative to pelagic production (Vasconcelos et al. 2016), altering the importance of different energy transfer pathways. This shift affects prey distribution and composition in both habitats, impacting prey availability to higher consumers. When predators such as fish, adjust their diet toward feeding on the relatively more abundant pelagic zooplankton, they exert top-down control which in turn can benefit pelagic primary producers via reduced grazing pressure (Vasconcelos *et al.* 2019). In addition to shifting the relative share of pelagic vs. benthic prey resources due to light limitation, increased t-OC also directly affects the balance between phytoplankton and bacterial production in the pelagic zone. Start from low levels, increased input of DOM and nutrients could initially benefit both phytoplankton and bacterial production by increasing nutrients that usually limit primary producer's biomass growth (Andersson et al. 2018). However, over time, continuous loading of DOC mainly benefits bacterial production, as bacteria can utilise DOC as an energy source, but suppresses phytoplankton growth due to light limitation and/or competition with bacteria, thereby shifting more of the total biomass production to the microbial loop (Jansson et al. 2007; Wikner and Andersson 2012). Importantly, external t-OC can support a significant portion of biomass production in both benthic and pelagic habitats (Ask et al. 2009).

Besides indirect effects of t-OC on fish biomass through changes in food availability, water darkening may also directly influence fish behaviour. Fish have well-developed eyes and most fish species depend a lot on their vision when receiving information from their environment (Guthrie 1986). Increased water turbidity and/or DOC, which alter underwater light climate, have been shown to directly affect the feeding behaviour of some zooplanktivorous fish species (Weidel et al. 2017). Similarly, strongly vision-dependent piscivorous predators are negatively affected by reduced visibility compared to fish feeding on benthic prey (Hecht and van der Lingen 1992). However, the overall negative impact of water darkening on fish biomass is likely driven by a combination of multiple factors and a literature synthesis by Roth et al. (2025) found no evidence that browning affects fish foraging in a consistent way across species. In most cases, it seems that reduced fish biomass in dark waters is more clearly linked to a decline in food availability rather than decreased foraging rates due to difficulties in detecting prey (Horppila *et al.* 2025), especially in species capable to forage efficiently even in low-light conditions, such as roach (*Rutilus rutilus*) (Van Dorst et al. 2020).

Direct and indirect effects of water darkening have been shown to affect individual fish body growth differently over ontogeny e.g. relating to ontogenetic diet shifts in prey. This was experimentally demonstrated by Van Dorst et al (2022) showing how browning decreased body growth of young-of-the year fish more than for 1 year-old fish. They explained this by a shift in zooplankton community

composition with browning and differences in prey selectivity among small and larger roach.

As illustrated by the examples above, water darkening can alter trophic interactions and prey availability, highlighting the complexity of natural aquatic food webs and the influence of both top-down and bottom-up controls. Bottom-up regulation refers to the control of energy flow to higher trophic levels by resource availability, such as nutrients and light (Weathers et al 2013). Increased t-OM and water darkening affect food webs from the bottom-up by reducing light attenuation and by shifting primary production from benthic to pelagic and further by favouring microbial heterotrophy over primary production (Ask et al. 2009; Wikner and Andersson 2012). Top-down control refers to organisms at higher trophic levels regulating biomasses of those at lower ones (Carpenter et al. 1985). Studies have shown how the effects of DOC on coastal food webs depend on the presence or absence of a top predator (Degerman et al. 2018, Garnier et al. 2025). Degerman et al. (2018) experimentally showed that in ecosystems where zooplankton represented the highest trophic level, an increase in DOC in the water correspondingly increased zooplankton production. However, in a system with fish, increased DOC had a negative effect on fish growth and production (Degerman et al. 2018). These findings highlight that water darkening and other ecosystem changes cannot be understood solely through simple top-down or bottom-up trophic cascade frameworks, but that we need to account for variation in food web structure and food chain length.

2.1.3 Effects of increased t-OC in pelagic habitat

The terms allochthonous (terrestrial origin) and autochthonous (fixated within the aquatic system) are commonly used to describe the origin of carbon in aquatic systems. In oligotrophic lakes and nutrient-poor marine ecosystems with low productivity, bacteria have been shown to significantly contribute to energy mobilization through the pelagic food webs by utilizing external sources of carbon, whereas phytoplankton dominates in more nutrient-rich waters (Gasol *et al.* 1997; Jansson et al. 2007). In oligotrophic systems, pelagic basal producers, particularly heterotrophic bacteria, rely on allochthonous carbon and nutrients originating from outside of the system (Ask et al. 2009) and the autochthonous carbon alone does not support high bacteria biomass and growth (Kritzberg *et al.* 2004). As a result of increased input of t-OC favouring bacteria that can use inorganic dissolved substances directly as a resource, leads to enhanced competition between phytoplankton and bacteria in the pelagic habitat (Andersson et al. 2015). In an ecosystem with higher loads of freshwater input and t-OC, basal pelagic production may therefore be dominated by heterotrophic bacteria (Wikner and Andersson 2012).

A large portion (common assumption being 90%, Lindeman 1942, but see Eddy *et al.* 2021 for why values likely are highly variable) of carbon fixed at the base of food webs is lost at each trophic level through respiration, sloppy eating and reproduction. Lower carbon losses imply a higher rate of energy transfer through the food web, leading to high food web efficiency (FWE). Ultimately, the combination of basal energy mobilization and FWE determines how many trophic levels, and thus top predators, aquatic system can sustain. High FWE values means that more energy is transferred from lower to higher trophic levels (Eddy *et al.* 2021). Generally, FWE tends to be low in oligotrophic waters (Sommer *et al.* 2002). In these low-nutrient ecosystems, primary production is dominated by picoplankton, which is too small to be directly consumed by meso-zooplankton. As a result, the carbon they fixate into the food web enters the microbial loop, passing through additional trophic links before reaching zooplankton and higher trophic level consumers (Sommer *et al.* 2002). In contrast, autotrophic algal primary production in systems dominated by meso-zooplankton has been shown to transfer energy more efficiently to higher trophic levels due to fewer trophic levels between primary production and top predators (Berglund *et al.* 2007), although under eutrophic conditions FWE may be low due to dominance of less edible primary producers (Garzke *et al.* 2019) As stated earlier, t-OC tends to benefit heterotrophic bacteria over phytoplankton production, leading to longer and less efficient food chains (Degerman *et al.* 2018). Consequently, FWE is expected to decrease, resulting in lower biomass production at higher trophic levels (Berglund *et al.* 2007).

2.2 Effects of warming on aquatic organisms

Environmental temperature is closely linked to individual physiology, especially in ectotherms, whose body temperature and thereby metabolism, is directly determined by their ambient conditions. According to the metabolic theory of ecology (MTE), temperature affects metabolic rates (Brown *et al.* 2004) and thus organisms net energy gain and body growth (Block 2024). Since metabolic rate is also influenced by body size, temperature and size together determine individual body growth, in turn, influencing fitness, maturation size and ultimately the efficiency of energy transfer across trophic levels (Barneche and Allen 2018). Not only can temperature and body size additively determine body growth, but both empirical and theoretical studies suggest that temperature effects are size-dependent. Studies have, for example, shown that warming accelerates the growth of juvenile fish but that the effect diminishes in larger and older individuals (Huss *et al.* 2019; Van Dorst *et al.* 2019; Lindmark *et al.* 2022; Ikpewe *et al.* 2021; Wootton *et al.* 2022). This size-specific response is often linked to a negative relationship between optimum growth temperature and body size, resulting from differences in

how maximum consumption and metabolic rates scale with temperature and body size. (Lindmark *et al.* 2022). The temperature-dependence of body growth is reflected in the temperature size rule (TSR) (Atkinson 1994), which suggests that ectotherms, including fish and most aquatic species, grow at a faster rate but mature earlier in warmer environments, resulting in smaller asymptotic body sizes (Forster *et al.* 2012, although not always true, see below). While higher temperatures are thought to reduce adult size by increasing size-dependent maintenance costs and speeding up maturation (Niu *et al.* 2023), recent findings suggest that fish populations can adapt metabolically over generations, potentially mitigating these effects (Wootton *et al.* 2022). However, we still lack a general understanding of mechanisms and key processes affecting body size-temperature responses (Verberk *et al.* 2021).

Shrinking body size in fish can have major ecological and economic consequences, especially in commercial fisheries where reduced body size and biomass of large predatory fish may lead to lower yield-per recruit (Audzijonyte *et al.* 2013) and thus overall lower fisheries catch (Lindmark *et al.* 2022b). Although many empirical studies support TSR in fish (e.g. Ikpewe *et al.* 2021), some studies have reported deviating results (Solokas *et al.* 2023; Audzijonyte *et al.* 2020) indicating that the effects of warming on individuals and populations are strongly influenced by local environmental factors and cannot always be universally predicted based solely on climatic variables (Solokas *et al.* 2023). At the population level, warming often results in smaller mean body size and reduced total biomass, even with increased growth rate (size-at-age) in juveniles (Baudron *et al.* 2022). In a study of lake fish populations across a large temperature gradient, Van Dorst *et al.* (2019) showed how mean body size and population biomass production decreased with temperature (van Dorst *et al.* 2019). However, like individual-level responses to higher temperatures, warming waters may not always lead to a decrease in population biomass production. For example, Solokas *et al.* (2023) found that populations with large-bodied individuals increased their size more than small-bodied populations in warming waters.

Although many studies on temperature-body size relationships exist specifically for fish, they are common across organism groups (Daufresne *et al.* 2009). Accordingly, also zooplankton communities often shift toward dominance of smaller species under climate change (Uszko *et al.* 2022). Within zooplankton species, however, warming may also drive a shift in population size and stage structure, with juvenile growth accelerating and resulting in biomass accumulation in adult life stages (Uszko *et al.* 2022). Consequently, not all species and individuals show the same size-specific responses to variation in temperature (Audzijonyte *et al.* 2020), highlighting the complexity of temperature effects on aquatic organisms and food webs.

2.3 Northern coastal food web responses to warming and darkening under climate change

In the Baltic Sea, surface water temperature is estimated to rise 2–4 °C and precipitation to increase ~30% by the end of the century (HELCOM 2023). At the same time, climate change is expected to increase the input of allochthonous organic matter into the coastal waters of northern Europe due to the increased precipitation (de Wit et al. 2016, Opdal et al. 2023). Still, we have limited knowledge about their combined effects on coastal food webs. Van Dorst et al. (2019), with a space-for-time approach suggested that ongoing browning of lakes will add to the negative effects of warming on fish production (van Dorst et al. 2019). In fish larvae, studies instead suggest that warming can increase body growth while darkening simultaneously decreases it (Huss et al. 2021). However, at the population level, accelerated juvenile growth rate does not necessarily result in higher total biomass, if the body growth and/or number of large individuals simultaneously decrease (van Dorst et al. 2019). This can also be expected as warming has been shown to increase mortality in fish (Lindmark et al. 2023). In conclusion, the net effect of climate warming on fish population structure and production depends on the balance between effects on growth and mortality, and the combined effects of warming, darkening and other concurrent changes.

In addition to the effects of warming-induced changes in body growth and size structure, fish production may suffer due to both reduced resource production and energy transfer efficiency (Mehner et al., 2022). A study by Pontevic et al. (2021) estimated that a decrease in primary production may lead to a decrease in total consumer biomass in marine environments by 18.5 % by end of the century. Similarly, water darkening and increased DOC concentrations are projected to favour bacteria production over phytoplankton production, resulting in longer food chains and therefore to further decline in energy transfer efficiency and thus biomass at upper trophic levels (Degerman et al. 2018). Warming and increased organic carbon loading may also contribute to the expansion of anoxic conditions in deep basins, by strengthening stratification and oxygen consumption, as well as internal nutrient release which may increase cyanobacteria production (Andersson *et al.* 2015). Both modelling and empirical studies suggest that water darkening influences food webs from the bottom-up by reducing light availability and thus benthic primary production and benthic resource availability for consumers, while simultaneously increasing nutrients in the pelagic habitat, which may favour pelagic production. In contrast, warming may to a larger extent affect aquatic food webs from top-down by affecting consumer feeding rates and size distributions (Van Dorst et al. 2019, Vasconcelos et al. 2019). However, how the combined effect of warming and darkening play out in terms of the relative importance of bottom-up vs. top-down control of coastal food web in natural systems is still unknown.

Not only are the effects of environmental change, such as warming and darkening, on food webs interesting from an ecological point of view but resulting shifts in food web structure and food chain length may crucially affect how contaminants bioaccumulate and transfer. Contributing factors that can affect the latter include food chain length, species diversity and individual's traits, such as lipid or muscle content, body size, age, gender, reproduction, habitat use, feeding preferences and trophic level (Borgå et al. 2004). Environmental changes, such as warming and increased organic matter input can alter food web structure and food chain length and thereby likely to influence contaminants transfer. To the best of my knowledge, no previous studies have examined how increased input of coloured organic matter, either independently or together with rising sea temperatures, influences radionuclide bioaccumulation and transfer. Understanding how climate change may alter these pathways and dynamics is essential for accurately simulating potential future accident scenarios. The Fukushima accident in 2011 further highlighted the need to better integrate ecological processes into radioecological models to improve predictions of radionuclide dynamics in natural environments (Vives I Batlle et al. 2018).

3. Anthropogenic radionuclides in aquatic ecosystems

3.1 Radionuclides

3.1.1 ^{137}Cs exposure in the Baltic Sea

Anthropogenic radionuclides (RN) refer to radioactive substances, such as ^{90}Sr , ^{137}Cs , ^{129}I and ^{14}C , which are continuously produced by human activities and do not naturally occur on Earth (Benitez-Nelson *et al.* 2018a). Among them, the focus in this essay is on cesium-137 (^{137}Cs , later referred to also as radiocesium), which is a fission product and a long-lived radionuclide with a physical half-life of 30.2 years. It is a widely studied and an important indicator of radioactive pollution in aquatic environments, especially due to its longer half-life compared to other radiocesium isotopes, such as ^{134}Cs , with a half-life of only 2.2 years (Lestaevel *et al.* 2010). ^{137}Cs emits high-energy beta particles, and its decay product, $^{137\text{m}}\text{Ba}$, emits gamma radiation (EPA, 2025). Although the long-term health impacts of ^{137}Cs exposure are not fully known, human studies have associated it with immune deficiency, deformations, neurological disorders and increased thyroid cancer risk, particularly in children, who are more vulnerable to toxic effects than adults (Lestaevel *et al.* 2010). Chemically, ^{137}Cs behaves similarly to the essential nutrient potassium (K) and it is water-soluble. This allows ^{137}Cs to be efficiently taken up by plants and animals and thus be transported through food chains (Ashraf *et al.* 2014).

Large quantities of anthropogenic radionuclides typically enter marine ecosystems through single point sources, often linked to one-time events or accidental releases rather than continuous emissions. However, continuously occurring authorised discharges of radioactive substances such as ^{60}Co and ^{137}Cs from nuclear power plants and research reactors contribute a small part of the total radioactivity load to the Baltic Sea (HELCOM 2013). On a global scale, the largest historical source of ^{137}Cs and other radionuclides are nuclear weapon testing between 1945 and 1980, which released an estimated 1 000 PBq of ^{137}Cs into the atmosphere, from which 600 PBq ended up in the oceans (Benitez-Nelson *et al.* 2018a). This weapon testing led to a widespread fallout particularly in the northern

hemisphere, with over 78 % of the total radioactivity distributing around the globe, and rest deposited near the test sites (Benitez-Nelson et al. 2018a). Other major sources of anthropogenic radionuclides include release from nuclear reprocessing facilities and accidents related to nuclear power plants, such as the Chernobyl disaster in Ukraine (April 1986) that released 85 PBq of ^{137}Cs globally and the Fukushima Dai-ichi incident in Japan (2011) with emissions around 20–40 PBq of ^{137}Cs (Benitez-Nelson *et al.* 2018a).

The anthropogenic radionuclide contamination levels in the Baltic Sea are among the highest globally (Ikäheimonen et al. 2009). This is due to the Baltic Sea's unique environment, including a large brackish water body with limited water exchange with the North Sea, shallow morphology and a drainage basin more than four times larger than the sea itself (HELCOM 2023). The elevated levels of ^{137}Cs in the Baltic Sea originate primarily from the Chernobyl disaster in 1986, which released a total of 4700 TBq of ^{137}Cs into the Baltic Sea region (Nielsen et al. 2010). Alongside strontium-90 (^{90}Sr) fallout from the same event, which together with ^{137}Cs are the main contributors to the Baltic Sea radioactivity, other relevant anthropogenic radionuclides include ($^{239+240}\text{Pu}$) and ^{99}Tc (Eriksson et al. 2018; Zalewska and Suplinska 2013). Due to weather conditions at the time of the accident and varying sedimentation rates, radionuclides have distributed unevenly in the sea area, with the highest ^{137}Cs concentrations found in the Bothnian Sea, the Gulf of Finland and specifically in coastal sediments (Kotilainen et al. 2021; Ikäheimonen et al. 2009). In addition to Chernobyl, other radiocesium sources to the Baltic Sea are the nuclear weapons testing and discharges from nuclear reprocessing plants outside of the Baltic Sea such as Sellafield in the UK and La Hague in France. By contrast, the 11 nuclear power plants located along the Baltic Sea coast contribute less than 0.1% of total radionuclide activity (Ikäheimonen et al. 2009).

It is worth noting that the ^{137}Cs activity in the Baltic Sea is steadily decreasing and no global increases in radionuclide concentrations after the Fukushima Daiichi nuclear accident have been detected in seawater (Eriksson et al. 2018). Due to the Baltic Sea's slow water exchange time, concentrations of ^{137}Cs in sea water has reached a nearly stable state and is nowadays impacted mainly by sedimentation, radioactive decay and bioaccumulation to biota (Bezhenar et al. 2016; Zalewska and Suplinska 2013). ^{137}Cs accumulation in biota has decreased its environmental concentrations in sea regions with high contamination (Burger and Lichtscheidl 2017). Given the importance and vulnerability of coastal ecosystems to climate warming, it is important to understand how such environmental change might influence ^{137}Cs accumulation and transfer in coastal food webs, including the combined effect of projected sea surface temperature increases of 0.4-0.6°C per decade (HELCOM 2023) along with increased precipitation bringing terrestrially derived organic material to coastal Baltic Sea areas.

3.1.2 Uptake, metabolism and excretion

Even though radiocaesium behaviour has been widely studied both in field and laboratory conditions, studies on uptake and transfer of ^{137}Cs through food webs have received various and contradicting results (Rowan and Rasmussen 1994). It is widely accepted that radionuclides, such as other contaminants, are transferred to organisms from the environment through several pathways (Ali and Khan 2019). In aquatic environments, depending on the organism, radionuclides can be taken up via three main routes: from the surrounding contaminated seawater, through ingestion of contaminated food or contact with contaminated sediment (Benitez-Nelson et al. 2018c). Following uptake via diet, radionuclides absorb through the gut wall into the internal tissues and cells. In addition to exposure and contamination through food, some radionuclides can also absorb through external surfaces such as scales, skin and gills. Adsorption is another key mechanism affecting radionuclide concentrations in particularly organisms with hard, calcified external body surfaces (e.g. crustaceans and echinoderms), where ionic charges attract and bind radionuclides into the external surfaces (Carvalho 2018). If transferred into a non-contaminated environment, aquatic organisms eliminate ingested radionuclides through biological processes such as excretion (Benitez-Nelson et al. 2018c) and desorption (Carvalho 2018).

Uptake and elimination dynamics are essential for determining **biological half-life**, which refer to the time it takes for half of the radionuclide to be eliminated from an organism through biological processes (Tanaka et al. 2018). The **effective half-life** is used to assess the overall accumulation of radionuclides. It combines the **physical half-life** (e.g. ~30 years for ^{137}Cs) with the biological half-life, reflecting both the radioactive decay and the organism's ability to eliminate the substances. The effective half-life thus represents the actual time required for the radionuclide concentration in the organism to be reduced by half. Consequently, effective half-lives vary significantly depending on the organism and environmental conditions (Metian et al. 2019). Therefore, results from the high-salinity marine environments in coastal Japan cannot be directly used to predict outcomes in the brackish Baltic Sea, where effective half-lives of ^{137}Cs are estimated to be 1–9 years longer (Takata 2022). According to the International Atomic Energy Agency (IAEA), the effective half-lives of ^{137}Cs and ^{90}Sr for the Baltic Sea as a whole are 14.1 years (^{137}Cs) and 12 years (^{90}Sr), respectively (Zalewska and Suplińska 2013).

The concentration of radionuclides in seawater is not necessarily directly correlated with concentrations measured in biota, as uptake processes are influenced by multiple environmental parameters, such as temperature effects on metabolic rates and ionic competition. In aquatic environments, radionuclides are

distributed both in dissolved form in the water column and bound to particles in sediments (Carvalho 2018). According to numerous studies following both the Fukushima Dai-ichi nuclear power plant accident and the Chernobyl disaster, the highest concentrations of radioactive cesium in aquatic environments are typically found in the sediments (Kotilainen et al. 2021). This is due to adsorption to organic particles, with ^{137}Cs concentrations in organic matter being up to seven times higher than in bulk sediment (Bezhenar et al. 2016). ^{137}Cs has a strong affinity to bind to fine clay particles, which are highly abundant in soils and soft sediment bottoms, and therefore accumulate more radionuclides than hard and coarse bottoms (Fuji et al. 2017; Eriksson et al. 2018). This is the case also in the Baltic Sea where, according to monitoring programmes, ^{137}Cs activity in the sediments are four times higher than in the seawater (Eriksson et al. 2018). As a result, sediments serve as a long-term storage and source for radionuclides in aquatic ecosystems globally, including in the Baltic Sea (Yamazaki 2020; Zalewska and Suplińska 2013).

Over time, most radionuclides in the water column are absorbed in suspended particulate matter composed from plankton, detritus and minerals, which eventually accumulate into sediments (Zalewska and Suplińska 2013). However, aquatic organisms can absorb a small fraction of radionuclides directly from the water (Ashraf et al. 2014). Therefore, water chemistry can significantly affect radionuclide uptake. For example, an increase of K^+ concentration in the water can result in a significant decrease of ^{137}Cs uptake in algae because ^{137}Cs is taken up by the same K transport channels in plant cell membranes (Ashraf et al. 2014). In addition, water colour and humic substances have been shown to influence ^{137}Cs concentration in fish. Särkkä et al. (1996) found that in high humic water lakes, ^{137}Cs concentration are lower in perch, which may be explained by radiocesium adsorption to humus particles, making it less available for biological uptake. However, the extent to which ecological processes contribute to these effects of humification are unknown. Also, salinity has been shown to have a significant effect on anthropogenic radionuclide concentration in waters by affecting the water solubility of radionuclides and the isotope exchange between water and bottom sediments, therefore directly influencing ^{137}Cs uptake by aquatic organisms (Mirzoeva et al. 2020). In isopods and macroalgae, lower salinity in the water has been shown to significantly increase ^{137}Cs accumulation, whereas bioaccumulation rates in fish were higher in salt water than in brackish water (Topcuoğlu 2000). Increased temperature has been seen to affect the concentration factor to fish muscle positively for some radionuclides, such as ^{137}Cs (Benitez-Nelson et al. 2018c; Nakahara et al. 1977), although this is not a consistent outcome among studies (Saiki and Koyanagi 1977). The pH on the other hand has not been found to have any effect on anthropogenic radionuclide concentration in water (Mirzoeva et al. 2020).

3.2 Bioaccumulation of radionuclides (^{137}Cs) in individuals

Bioaccumulation refers to the process by which a substance accumulates in an organism through uptake from the environment and via diet. If the rate of uptake exceeds the rate of elimination and growth dilution (i.e. contamination levels decreasing with increasing new biomass production) the substance accumulates over time, leading to an increasing concentration in the organism (Ali and Khan 2019). In the case of ^{137}Cs , over 70 % of the radionuclide accumulates in the fish muscle tissue after absorption. The remaining 30% is distributed among the gastrointestinal (11 %), skin or scales (9 %), bones (3%) and gills, liver and reproductive organs (4 %). Not all radionuclides, however, accumulate to the same organs, for example strontium-90 (^{90}Sr) shows a more even distribution within the organism: ~38 % accumulate in bones, 37 % in gastrointestinal organs and the remaining 18 % in skin or scales (Benitez-Nelson et al. 2018c). These differences in accumulation can be explained by the chemical similarities with other elements in the periodic table. As mentioned earlier, radiocesium has a chemical similarity to the essential nutrient potassium (K), and therefore its uptake to cells and tissues in solution uses the same pathway as potassium. Correspondingly, strontium shares chemical similarities with calcium (Ca) and therefore uses the same transfer pathways as calcium (Ashraf et al. 2014). Body shape can also be an essential factor influencing radionuclide accumulation. For example, in marine invertebrates, the variation in bioaccumulation among tissues depends on species. For species with flatter shaped shells, and therefore a high shell surface ratio, such as oysters, they tend to accumulate higher concentrations of radiocesium than more round-shaped clams (Metian et al. 2016).

To help understand radionuclide exposure pathways in aquatic organisms, specific metrics have been developed to model radionuclide fate and biological transport (Wang et al. 2000). Three commonly used parameters in such models are the concentration factor (CF), the transfer factor (TF) and the assimilation efficiency (AE). When applying these parameters, it is important to remember that they are generally developed under steady-state conditions and therefore depend strongly on environmental factors such as temperature, salinity and possibly also particulate and dissolved organic matter. Moreover, these parameters are species-specific, and values can differ substantially among closely related taxa and even within species if their habitats, feeding habits or environmental conditions differ significantly (Wang et al. 2000; IAEA 2004).

The concentration factor describes the ratio between radionuclide activity in the organism and that in the surrounding seawater (Benitez-Nelson et al. 2018c):

$$CF = \frac{Bq\ g^{-1}\ organism\ wet\ weight}{Bq\ g^{-1}\ sea\ water}$$

The transfer factor describes the ratio between radionuclide activity in the organisms and the sediment or food (Benitez-Nelson et al. 2018c):

$$TF = \frac{Bq\ g^{-1}\ organism\ wet\ weight}{Bq\ g^{-1}\ sediment\ or\ food}$$

The assimilation efficiency is typically determined under laboratory conditions with radiotracer experiments. It describes the proportion of an ingested radionuclide that is absorbed across the gut to the body tissues (Benitez-Nelson et al. 2018c). Assimilation efficiency therefore quantifies the bioavailability of radionuclides from the diet. For many animal taxa, the assimilation efficiency of ^{137}Cs is relatively high, reflecting the strong affinity of radiocesium to bind to internal tissues (Thomas et al. 2018; Zhao & Wang 2001), which could lead to biomagnification of radiocesium in food webs. Similar to concentration factors, AE values of ^{137}Cs are generally increase at higher trophic levels (Zhao & Wang 2001). Attempts to determine CF and AE values across different species have generated variable results (e.g. Topcuoğlu 2001), highlighting that species-specific physiology, feeding behaviour and environmental conditions can strongly influence radionuclide assimilation. Consequently, several mechanisms underlying ^{137}Cs uptake in lower trophic levels remain poorly understood (Metian et al. 2019).

Individual's own characteristic such as size, species and age can all influence bioaccumulation of ^{137}Cs , with size and age typically being strongly correlated. In one study, ^{137}Cs concentration in fish increased with length and weight in 4 out of 16 studied species (Kasamatsu and Ishikawa 1997). However, different species accumulate ^{137}Cs differently, and for some ray-finned fish, higher CFs of ^{137}Cs were found for smaller rather than for larger individuals, showing their ability to accumulate ^{137}Cs more efficiently (Metian et al. 2019). This kind of variation is usually related to their use of different food resource and variation in metabolic activity (Thomas & Fisher 2019). Looking specifically at between-species variation in the Baltic Sea, perch seem to accumulate high levels of radiocesium, including relatively small non-piscivorous individuals, compared to other fish species occupying similar trophic levels (Sundbom et al. 2003).

Age has been shown to influence bioaccumulation in fish, and older fish generally contain higher levels of ^{137}Cs than juveniles (Kryshev and Ryacov 2000). However, in the case of a sudden, single-point exposure, the situation can be reversed due to younger size classes accumulating radiocesium more actively than older fish and reaching maximum levels faster. This was seen after the Chernobyl accident, with juvenile fish containing higher concentrations than the older individuals (Kryshev and Ryacov 2000). Nevertheless, juveniles also lost radiocesium in their tissues faster than older individuals when living in an environment with decreasing radiocesium activities due to their higher metabolism

per unit biomass, with their radiocesium levels following the contamination in their food (Kryshev and Ryacov 2000). Many fish species, such as Eurasian perch undergo one or several ontogenetic niche shift through its life cycle. Juvenile perch start to feed on pelagic zooplankton, then later shift to benthic macroinvertebrates and eventually, when large enough, also feed on fish (Hjelm et al. 1999). This leads to shifts in species interactions and influences not only the whole food web structure and dynamics but likely also radiocesium transport, adding to differences of bioaccumulation between differently sized perch. In the case of perch, large individuals feeding on higher trophic level diet items are therefore likely to contain higher levels of radiocesium.

The effects of warming and temperature variation on bioaccumulation is still relatively unknown. In nature, species living in warm regions have generally not been shown to accumulate radiocesium differently than species in colder environments (Metian et al. 2016). In experimental set ups, determination of ^{137}Cs bioaccumulation and concentration factors has, however, shown that temperature can influence the accumulation rate by increasing uptake rates in clams and fish, but not in gastropod species (Thomas & Fisher 2019). Pan and Wang (2016) accordingly found that higher experimental temperatures affect ^{137}Cs uptake to fish due to their increased metabolic activity in warmer waters. Interestingly, bioaccumulation rates in macroalgae can be negatively correlated with temperature (Topcuoğlu 2001).

3.3 Transfer of radionuclides (^{137}Cs) in food webs

Understanding how radiocesium bioaccumulate in single individuals or species is not enough to understand its transfer in food webs. For ^{137}Cs concentration in fish, studies have shown that the most significant source ($\geq 99\%$) of ^{137}Cs is from their diet (Thomas et al. 2018), and that only a small fraction is absorbed through gills or scales directly from the water (Metian et al. 2016; Yamazaki 2020). In addition, trophic pathways are shown to be a main uptake route of ^{134}Cs for shrimps and bivalves (Metian et al. 2016). All aquatic organisms acquire some radiocesium directly from the seawater, but this accounts for only 1.2–2.5% of their total body burden, leading that nearly all accumulated radiocesium to consumers is ingested through their diet (Wang et al. 2016). Therefore, understanding food web structure and trophic interactions are essential to understand how radiocesium is transported in coastal food webs. Natural aquatic food webs are complex and influenced by multiple factors, making modelling of these systems challenging both with respect to ecological interactions and contaminant transfer. In addition to this challenge, already gathered knowledge on the topic and studies taking ecological interactions

into account, especially with respect to ^{137}Cs transfer from sediments up the food chain, are still limited (Periáñez et al. 2019).

When examining ecological processes and trophic interactions, including at higher trophic levels, it is important to consider that the structure of the food web at the level of basal producers strongly influences biomass distribution and consequently radionuclide bioaccumulation to higher levels (Rowan and Rasmussen 1994). For radionuclide bioaccumulation in general, and for ^{137}Cs bioaccumulation specifically, several studies have shown that the primary route of ^{137}Cs into organisms varies with trophic level (Yamakazi 2020; Wang et al. 2016). Phytoplankton and zooplankton take up ^{137}Cs mainly from the surrounding water via sorption (adsorption and/or absorption) (Thomas et al. 2018). For primary producers, such as phytoplankton, CF values for ^{137}Cs are generally low, suggesting that radiocesium accumulates very little in their tissues (Wang et al. 2000; Thomas et al. 2018). Because phytoplankton forms the main food resource for filter-feeding organisms such as bivalves and zooplankton, them feeding solely on phytoplankton would be expected to result in low radiocesium transfer through their diet. However, high ^{137}Cs concentrations have been measured in many benthic environments where bivalves live (Fuji et al. 2018). If the environment is disturbed and sediment is resuspended and further ingested by the bivalves in large quantities, this would increase ^{137}Cs concentrations in bivalves. Bivalves that are used as a key food resource for other aquatic species, such as predatory gastropods, can facilitate the transfer of radiocesium to further up in food web (Bezhenar et al. 2016; Wang et al. 2000; Wang et al. 2016). This is supported by Wang et al. (2025), who in a laboratory experiment found that radiocesium can be transferred to benthic animals feeding on organic particles in the sediment, which in turn are eaten by predatory macroinvertebrates. They also showed that radiocesium was passed to next trophic level with high efficiency. However, the sediment composition and the bioavailability of ^{137}Cs to benthic invertebrates strongly influence how much of it that can be taken up by the animals. For example, has a high affinity of ^{137}Cs to particulate matter, particularly to clay, decreases assimilation efficiency from sediment to chironomid larvae (Fuji et al. 2017). Consequently, not all benthic invertebrates exposed to contaminated sediment will necessarily accumulate high levels of radiocesium. Their ^{137}Cs uptake can vary with habitat use and with how the ingested ^{137}Cs binds to particulate matter that passes through organisms' digestive tract (Fujino et al. 2017). Therefore, environmental radioactivity levels, species interactions and sediment characteristics all need to be considered when modelling radionuclide transfer in food webs.

Because organisms at higher trophic levels generally grow larger and consume more radionuclide containing prey, the transfer factor tends to increase with trophic level (Wang et al. 2000). At the same time, ^{137}Cs turnover rate decreases with trophic level (Wang et al. 2016). For example, gastropods and bivalves have a

relatively higher depuration (a term commonly used for shellfish to describe the removal of contaminants in their gut when moved to uncontaminated environment) effectiveness than fish. For polychaetes, ^{137}Cs dietary uptake elimination rate was 45%, for crabs 14%, but for fish only 5% per day (Wang et al. 2016).

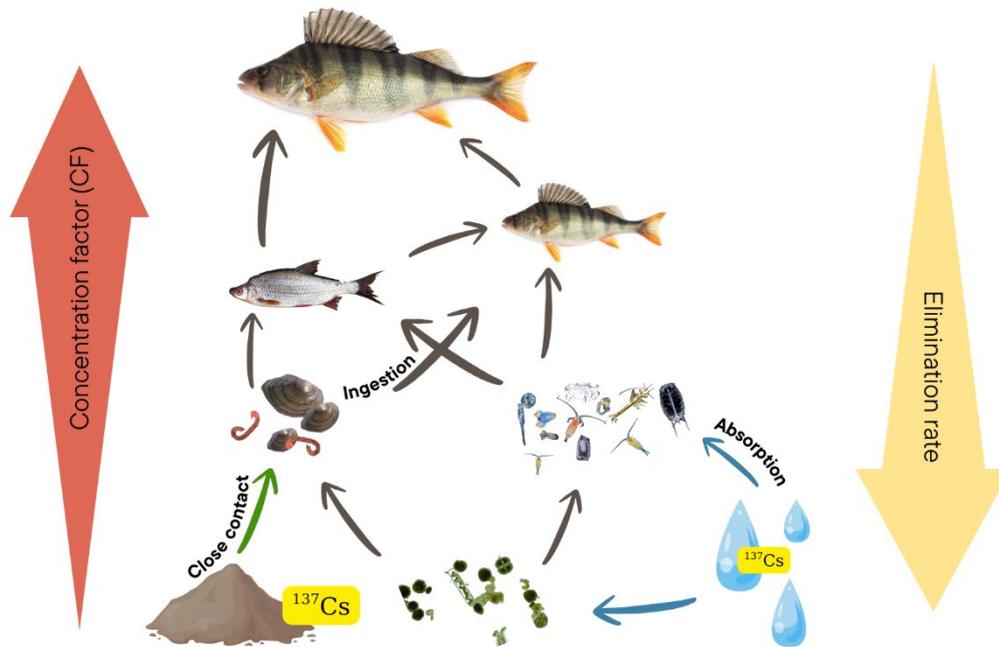


Figure 1. Different pathways of ^{137}Cs to large piscivorous perch in a schematic coastal food web. Concentration factors generally increase when moving up the food chain, whereas elimination rates generally increase when moving down.

When the contaminant concentration increases with increasing trophic level, this is called biomagnification. It is often caused by the long effective half-life of contaminants in organism and when organisms are continuously exposed and are ingesting contaminated prey (Ali and Khan 2019). However, numerous studies on the matter have reported varying results, both for and against the tendency of ^{137}Cs to biomagnify in food chains. For example, Rowan et al. (1998) and Kasamatsu and Ishikawa (1997) showed that ^{137}Cs concentration increased almost four-fold at each trophic level in Ottawa river and in average three-fold in their entire dataset. Also Pan and Wang (2016) showed that ^{137}Cs has a strong potential to biomagnify in estuarine food webs. However, not all studies found this general trend for radiocesium CF to increase with increasing trophic level (Metian et al. 2019). ^{137}Cs biomagnification can thus vary between ecosystems, species, populations and even within individuals, highlighting the need to examine these variations together with environmental characteristics to understand outcomes (Leaphart et al. 2019).

As mentioned earlier, diet is one of the most important factors contributing to variation in ^{137}Cs concentration in consumers. Rowan and Rasmussen (1994) reported that piscivorous fish generally bioaccumulate more radiocesium than fish

feeding on zooplankton (planktivores) and benthic invertebrates (benthivores), although they also found cases when this was not true. In a later study, Rowan et al. (1998) found that fish with a diet consisting mainly of benthic invertebrates had two times higher ^{137}Cs levels than planktivorous fish of the same trophic level. Similarly, Sundbom et al. (2003) demonstrated biomagnification of radiocesium in piscivorous fish, but they did not find a relationship between trophic level and radiocesium levels in non-piscivorous fish. They explained this with a difference in their food sources, where algae and invertebrates tend to be in equilibrium with the ambient ^{137}Cs concentration. The length of the food chain is thus an important factor with diet affecting how much fish and other top predators, including those commonly used as human food, accumulate ^{137}Cs . Still, as pointed out above, there is variation also within trophic levels, with e.g. perch being shown to have a higher ^{137}Cs concentrations compared with some other fish species at the same trophic level (Sundbom et al. 2003).

Biodilution is the opposite phenomenon to biomagnification, where the studied substance concentration decreases with trophic level (Ali and Khan 2019). However, although this is possible for some contaminants, numerous studies have shown that ^{137}Cs does not biodilute but rather increases in concentration higher up in the food chain (Heldal et al. 2003; but see Metian et al. 2019).

3.4 River runoffs effects on radionuclide bioavailability

From the atmosphere, radiocesium along with other radioactive gasses emitted from point sources, such as nuclear accident or weapon testing sites, eventually deposit to land or water. Depending on soil type, radiocesium is absorbed tightly into clay particles (Yamazaki 2020) and after fixation does not really move in the environment but commonly stay in the top 20 cm soil layer (Isaksson and Erlandsson 1998). This is due to ^{137}Cs strong tendency to attach itself to clay particles, found in both sediments and terrestrial soils. In addition, clay particles play an essential role in radionuclides transfer processes from soils to coastal waters (Yamazaki 2020). In the environment, radiocesium is usually present in two main forms; dissolved and particulate. Dissolved is generally present as cesium ions and cesium ion hydrates, which are more mobile and thus available for uptake by plant roots. The particulate form is more stable and tightly bounded into suspended solids (Tsuji et al. 2014).

During summer months with high rainfall and flood events, dissolved radiocesium can be remobilized from the upper soil layer and move to the deeper soil layers (Isaksson and Erlandsson 1998). Dissolved ^{137}Cs can also be leached from leaf litter and transported with terrestrial material along streams and rivers to seas and oceans. Leaf litter has been shown to be one of the main sources of

radiocesium to aquatic environments (Gomi et al. 2018). Therefore, vegetation and land-use close to rivers and streams have a central role in radionuclide transportation. According to monitoring studies done in forest areas close to Fukushima, Japan, dense tree stands are key sources of dissolved radiocesium to rivers (Iwagami *et al.* 2019). Concentrations of ^{137}Cs bound to terrestrial particles in rivers were, however, shown to be highly variable depending on disturbance caused by high flooding events and precipitation (Tsuji et al. 2014).

As for the Baltic Sea, about 70 % of ^{137}Cs is stored in sediments (Kotilainen et al. 2021). Although radioactivity of ^{137}Cs in the Baltic Sea is declining, it is still higher compared to pre-Chornobyl levels, especially in the coastal areas (Eriksson et al. 2018). The Baltic Sea sediments are generally rich in clay particles, making it efficient in storing ^{137}Cs , but at the same time decreases the bioavailability of dissolved ^{137}Cs to biota (Ikäheimonen et al. 2009). Although strong rainstorm events have been shown an increase dissolved ^{137}C concentrations in stream water, a case study of a flood in 1997 in the Southern Baltic Sea did not find an increase in radionuclides transported from eroded soil particles (Knapinska-Skiba et al. 2003). However, in theory, a climate-induced increase in precipitation could be expected to lead to more radionuclides being transferred to rivers and on to estuaries along with terrestrially derived organic matter, although this has not been explicitly studied.

4. Importance of understanding radionuclide bioaccumulation in changing environments

Radiation risk assessments evaluate the risks caused by exposure to ionizing radiation, and is a continuously evolving field relying primarily on long-time series of data of exposed populations (Nair 2023). Relying on long-time data series and field observations, however, has its own limitations, e.g. as this can only tell us about how radionuclides behave in a studied system for a certain period and do not take into consideration continuous and future changes in environmental conditions (Avila et al. 2013). Numerous radioecological models based on measurement data, taking a variety of environmental conditions into consideration, have been developed to predict radionuclide behaviour and in aquatic environments (Almahayni et al. 2019). These models can aid understanding of radionuclide bioaccumulation rates, pathways to individuals of different species at various trophic levels in food webs. Still, to further these predictions, there is a need to consider more ecological processes in aquatic radioecology (Vives I Batlle et al. 2018). Ecological knowledge combined with insights on radionuclide behaviour can be used to simulate potential accident scenarios where large number of radionuclides is released into the atmosphere, detailing how it might be transported in the environment and accumulate into biota (Avila et al. 2013). Following the Fukushima accident in 2011, models were applied to predict radionuclides transport in the surrounding environment and valuable lessons were learned about the importance and limitations of predictive modelling. To develop modelling approaches to predict radionuclide bioaccumulation, taking ecological interactions into account, is therefore crucial for assessing the radiological risks and for supporting decision-making in safety regulations both now and in the future. This is especially important in a changing climate, which may alter food web composition, radionuclide transport pathways and ecological dynamics (Almahayni et al. 2019).

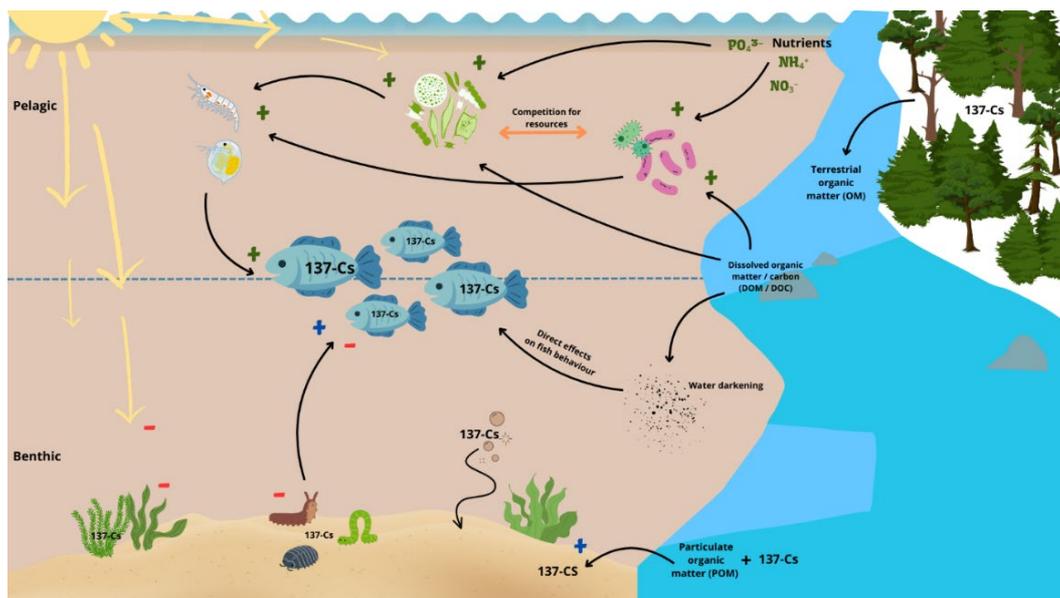


Figure 2. Transfer of ^{137}Cs in coastal ecosystems from land to the aquatic environments. Land use is a key factor affecting transport of ^{137}Cs bonded to terrestrial organic matter containing mineral particles. In marine ecosystems, sediments act as a radiocesium storage and as a main source of radionuclides to marine food webs through benthic invertebrates ingesting organic particles. Water darkening following increased loading of brown-coloured DOC is expected to shift fish prey resource use from benthic to pelagic and to favour heterotrophic bacterial production, leading to transfer across additional trophic levels from basal resources to fish.

Precipitation at northern latitudes, such as in Scandinavia, is expected to increase in the future due to climate change (Dore, 2005; Cooley et al. 2022). Due to increased precipitation, more organic material from terrestrial environments (e.g. leaf litter, upper soil layers and dead plant material) is transported to and along the river streams to coastal waters, causing darkening of the water (Opdal et al. 2023). As described above, darker water colour has been shown to significantly decrease benthic productivity, and especially if leading to anoxic conditions, result in a strong decrease in macroinvertebrates (Brothers et al. 2014). In this case fish might shift to rely more on the pelagic habitat and associated resources (Vasconcelos et al. 2018). This shift in fish diet can decrease the fish exposure to ^{137}Cs , given that the diet is the most significant pathway of ^{137}Cs accumulation to consumers (Thomas et al. 2018; Wang et al. 2016). Fish feeding on benthic invertebrates containing higher levels of ^{137}Cs due to their proximity to sediment, are likely to contain higher concentration of ^{137}Cs than fish feeding on zooplankton (Wang et al. 2016).

In addition to indirect effects of water darkening on ^{137}Cs bioaccumulation in fish via changes in dietary pathways, they may also be affected by direct effects of increased terrestrial carbon loading. The highest dissolved ^{137}Cs concentrations in Japan have been measured in forested areas during high rain and run-off events when dissolved ^{137}Cs can be released from solids such as sediment or leached from

leaf litter. This has been shown to be one of the main sources of ^{137}Cs to aquatic environments (Gomi et al. 2018). Therefore, increased precipitation can also directly affect ^{137}Cs concentrations in the environment and thus increase concentrations also in biota.

Not only may climate change modify contaminant uptake and bioaccumulation via changes in environmental concentrations and species composition but also by its effects on individual organisms. In some species, such as perch, body size is a significant factor affecting ^{137}Cs accumulation to individuals, with bigger ones usually containing higher levels than smaller ones (Sundbom et al. 2003). In warming environments, fish communities are expected to shift toward a dominance of smaller and younger individuals (Van Dorst et al. 2019, but see Lindmark et al. 2023), although these fish often exhibit faster growth rates at small sizes (Huss et al. 2019, Lindmark et al. 2022). Given the strong link between contaminant bioaccumulation and body size, such changes may be critical for predicting future radionuclide concentrations in fish. However, to date, there are no published studies that I know of addressing exactly how temperature will influence food web dynamics and thus contaminant dynamics up to fish.

Several previous studies have focused on ^{137}Cs transportation in the environment and the factors affecting its bioavailability to biota, especially following the Daiichi Nuclear incident in 2011 and the 1986 Chernobyl accident in the Baltic Sea. However, there is still no consensus on if and how ^{137}Cs bioaccumulate and biomagnify in food webs, and little is known about the role of ecological interactions in the transfer of ^{137}Cs between organisms, particularly under climate change scenarios.

References

- Ali, Hazrat, and Ezzat Khan. 'Trophic Transfer, Bioaccumulation, and Biomagnification of Non-Essential Hazardous Heavy Metals and Metalloids in Food Chains/Webs— Concepts and Implications for Wildlife and Human Health'. *Human and Ecological Risk Assessment: An International Journal* 25, no. 6 (18 August 2019): 1353–76. <https://doi.org/10.1080/10807039.2018.1469398>.
- Allan, J. David, María M. Castillo, and Krista A. Capps. 'Primary Producers'. In *Stream Ecology: Structure and Function of Running Waters*, edited by J. David Allan, María M. Castillo, and Krista A. Capps, 141–76. Cham: Springer International Publishing, 2021. https://doi.org/10.1007/978-3-030-61286-3_6.
- Almahayni, Talal, Nicholas A. Beresford, Neil M. J. Crout, and Lieve Sweeck. "Fit-for-Purpose Modelling of Radiocaesium Soil-to-Plant Transfer for Nuclear Emergencies: A Review." *Journal of Environmental Radioactivity* 201 (May 2019): 58–66. <https://doi.org/10.1016/j.jenvrad.2019.01.006>.
- Andersson, A., S. Brugel, J. Paczkowska, O. F. Rowe, D. Figueroa, S. Kratzer, and C. Legrand. 'Influence of Allochthonous Dissolved Organic Matter on Pelagic Basal Production in a Northerly Estuary'. *Estuarine, Coastal and Shelf Science* 204 (1 May 2018): 225–35. <https://doi.org/10.1016/j.ecss.2018.02.032>.
- Andersson, Agneta, H. E. Markus Meier, Matyas Ripszám, Owen Rowe, Johan Wikner, Peter Haglund, Kari Eilola, et al. 'Projected Future Climate Change and Baltic Sea Ecosystem Management'. *Ambio* 44 Suppl 3, no. Suppl 3 (June 2015): 345–56. <https://doi.org/10.1007/s13280-015-0654-8>.
- Angilletta, Michael J., Todd D. Steury, and Michael W. Sears. 'Temperature, Growth Rate, and Body Size in Ectotherms: Fitting Pieces of a Life-History Puzzle'. *Integrative and Comparative Biology* 44, no. 6 (December 2004): 498–509. <https://doi.org/10.1093/icb/44.6.498>.
- Ashraf, Muhammad Aqeel, Akib ,Shatirah, Maah ,Mohd. Jamil, Yusoff ,Ismail, and Khaled S. and Balkhair. 'Cesium-137: Radio-Chemistry, Fate, and Transport, Remediation, and Future Concerns'. *Critical Reviews in Environmental Science and Technology* 44, no. 15 (3 August 2014): 1740–93. <https://doi.org/10.1080/10643389.2013.790753>.
- Ask, Jenny, Jan Karlsson, Lennart Persson, Per Ask, Pär Byström, and Mats Jansson. 'Whole-Lake Estimates of Carbon Flux through Algae and Bacteria in Benthic and

- Pelagic Habitats of Clear-Water Lakes'. *Ecology* 90, no. 7 (2009): 1923–32. <https://doi.org/10.1890/07-1855.1>.
- Ask, Jenny, Owen Rowe, Sonia Brugel, Mårten Strömgren, Pär Byström, and Agneta Andersson. 'Importance of Coastal Primary Production in the Northern Baltic Sea'. *Ambio* 45, no. 6 (1 October 2016): 635–48. <https://doi.org/10.1007/s13280-016-0778-5>.
- Atkinson, D. (1994) Temperature and organism size—a biological law for ectotherms? *Advances in Ecological Research*, 25, 1–58.
- Audzijonyte, Asta, Anna Kuparinen, Rebecca Gorton, and Elizabeth A. Fulton. 'Ecological Consequences of Body Size Decline in Harvested Fish Species: Positive Feedback Loops in Trophic Interactions Amplify Human Impact'. *Biology Letters* 9, no. 2 (23 April 2013): 20121103. <https://doi.org/10.1098/rsbl.2012.1103>.
- Audzijonyte, Asta, Diego R. Barneche, Alan R. Baudron, Jonathan Belmaker, Timothy D. Clark, C. Tara Marshall, John R. Morrongiello, and Itai van Rijn. 'Is Oxygen Limitation in Warming Waters a Valid Mechanism to Explain Decreased Body Sizes in Aquatic Ectotherms?' *Global Ecology and Biogeography* 28, no. 2 (2019): 64–77. <https://doi.org/10.1111/geb.12847>.
- Audzijonyte, Asta, Shane A. Richards, Rick D. Stuart-Smith, Gretta Pecl, Graham J. Edgar, Neville S. Barrett, Nicholas Payne, and Julia L. Blanchard. 'Fish Body Sizes Change with Temperature but Not All Species Shrink with Warming'. *Nature Ecology & Evolution* 4, no. 6 (June 2020): 809–14. <https://doi.org/10.1038/s41559-020-1171-0>.
- Avila, Rodolfo, Ulrik Kautsky, Per-Anders Ekström, Per-Gustav Åstrand, and Peter Saetre. "Model of the Long-Term Transport and Accumulation of Radionuclides in Future Landscapes." *AMBIO* 42, no. 4 (2013): 497–505. <https://doi.org/10.1007/s13280-013-0402-x>.
- Barneche, Diego R., and Andrew P. Allen. 'The Energetics of Fish Growth and How It Constrains Food-Web Trophic Structure'. *Ecology Letters* 21, no. 6 (2018): 836–44. <https://doi.org/10.1111/ele.12947>.
- Bartels, Pia, Jenny Ask, Agneta Andersson, Jan Karlsson, and Reiner Giesler. 'Allochthonous Organic Matter Supports Benthic but Not Pelagic Food Webs in Shallow Coastal Ecosystems'. *Ecosystems* 21, no. 7 (1 November 2018): 1459–70. <https://doi.org/10.1007/s10021-018-0233-5>.
- Baudron, Alan R., Coby L. Needle, Adriaan D. Rijnsdorp, and C. Tara Marshall. 'Warming Temperatures and Smaller Body Sizes: Synchronous Changes in Growth of North Sea Fishes'. *Global Change Biology* 20, no. 4 (2014): 1023–31. <https://doi.org/10.1111/gcb.12514>.
- Benitez-Nelson, C.R., Buesseler, K., Dai, M., Aoyama, M., Casacuberta, N., Charmasson, S., Godoy, J.M., Johnson, A., Maderich, V., Masqué, P., Moore, W., Morris, P.J. & Smith, J.N. (2018a). Radioactivity in the Marine Environment:

- Cosmogenic and Anthropogenic Radionuclides. *Limnology and Oceanography e-Lectures*, 8 (1), 114–169. <https://doi.org/10.1002/loe2.10008>
- Benitez-Nelson, C.R., Buesseler, K., Dai, M., Aoyama, M., Casacuberta, N., Charmasson, S., Johnson, A., Godoy, J.M., Maderich, V., Masqué, P., Moore, W., Morris, P.J. & Smith, J.N. (2018c). Radioactivity in the Marine Environment: Understanding the Basics of Radioactivity. *Limnology and Oceanography e-Lectures*, 8 (1), 1–58. <https://doi.org/10.1002/loe2.10010>
- Berglund, Johnny, Umut Müren, Ulf Båmstedt, and Agneta Andersson. ‘Efficiency of a Phytoplankton-Based and a Bacterial-Based Food Web in a Pelagic Marine System’. *Limnology and Oceanography* 52, no. 1 (2007): 121–31. <https://doi.org/10.4319/lo.2007.52.1.0121>.
- Bernhardt, E. S., J. B. Heffernan, N. B. Grimm, et al. “The Metabolic Regimes of Flowing Waters.” *Limnology and Oceanography* 63, no. S1 (2018): S99–118. <https://doi.org/10.1002/lno.10726>
- Bezhenar, Roman, Kyung Tae Jung, Vladimir Maderich, Stefan Willemsen, Govert de With, and Fangli Qiao. ‘Transfer of Radiocaesium from Contaminated Bottom Sediments to Marine Organisms through Benthic Food Chains in Post-Fukushima and Post-Chernobyl Periods’. *Biogeosciences* 13, no. 10 (23 May 2016): 3021–34. <https://doi.org/10.5194/bg-13-3021-2016>.
- Block, B. A. ‘Endothermy in Tunas, Billfishes, and Sharks’. In *Encyclopedia of Fish Physiology (Second Edition)*, edited by Sarah L. Alderman and Todd E. Gillis, 529–36. Oxford: Academic Press, 2024. <https://doi.org/10.1016/B978-0-323-90801-6.00092-6>.
- Borowitzka, M. A., Lavery, P. S., & Keulen, M. (2006). Epiphytes of seagrasses. *Seagrasses: Biology, ecology and conservation*, 441-461. https://doi.org/10.1007/978-1-4020-2983-7_19
- Borum, Jens, and Kaj Sand-Jensen. ‘Is Total Primary Production in Shallow Coastal Marine Waters Stimulated by Nitrogen Loading?’ *Oikos* 76, no. 2 (1996): 406–10. <https://doi.org/10.2307/3546213>.
- Brown, James H., James F. Gillooly, Andrew P. Allen, Van M. Savage, and Geoffrey B. West. ‘Toward a Metabolic Theory of Ecology’. *Ecology* 85, no. 7 (2004): 1771–89. <https://doi.org/10.1890/03-9000>.
- Burger, Anna, and Irene Lichtscheidl. “Stable and Radioactive Cesium: A Review about Distribution in the Environment, Uptake and Translocation in Plants, Plant Reactions and Plants’ Potential for Bioremediation.” *Science of The Total Environment* 618 (March 2018): 1459–85. <https://doi.org/10.1016/j.scitotenv.2017.09.298>.
- Carpenter, Stephen R., James F. Kitchell, and James R. Hodgson. “Cascading Trophic Interactions and Lake Productivity: Fish Predation and Herbivory Can Regulate Lake Ecosystems.” *BioScience* 35, no. 10 (1985): 634–39. <https://doi.org/10.2307/1309989>.

- Carvalho, Fernando P. ‘Radionuclide Concentration Processes in Marine Organisms: A Comprehensive Review’. *Journal of Environmental Radioactivity*, II International Conference on Radioecological Concentration Processes (50 years later), 186 (1 June 2018): 124–30. <https://doi.org/10.1016/j.jenvrad.2017.11.002>.
- Cibic, Tamara, Laura Baldassarre, Federica Cerino, Cinzia Comici, Daniela Fornasaro, Martina Kralj, and Michele Giani. ‘Benthic and Pelagic Contributions to Primary Production: Experimental Insights From the Gulf of Trieste (Northern Adriatic Sea)’. *Frontiers in Marine Science* 9 (9 June 2022). <https://doi.org/10.3389/fmars.2022.877935>.
- Cooley, S., D. Schoeman, L. Bopp, P. Boyd, S. Donner, D.Y. Ghebrehiwet, S.-I. Ito, W. Kiessling, P. Martinetto, E. Ojea, M.F. Racault, B. Rost, and M. Skern-Mauritzen, 2022: Oceans and Coastal Ecosystems and Their Services Supplementary Material. In: Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Available from <https://www.ipcc.ch/report/ar6/wg2/>.
- Daufresne, Martin, Kathrin Lengfellner, and Ulrich Sommer. ‘Global Warming Benefits the Small in Aquatic Ecosystems’. *Proceedings of the National Academy of Sciences* 106, no. 31 (4 August 2009): 12788–93. <https://doi.org/10.1073/pnas.0902080106>.
- de Wit, H. A., Valinia, S., Weyhenmeyer, G. A., Futter, M. N., Kortelainen, P., Austnes, K., Hessen, D. O., Råike, A., Laudon, H., & Vuorenmaa, J. (2016). Current Browning of Surface Waters Will Be Further Promoted by Wetter Climate. *Environmental Science & Technology Letters*, 3(12), 430–435. <https://doi.org/10.1021/acs.estlett.6b00396>
- Degerman, R., R. Lefébure, P. Byström, U. Båmstedt, S. Larsson, and A. Andersson. ‘Food Web Interactions Determine Energy Transfer Efficiency and Top Consumer Responses to Inputs of Dissolved Organic Carbon’. *Hydrobiologia* 805, no. 1 (1 January 2018): 131–46. <https://doi.org/10.1007/s10750-017-3298-9>.
- Donadi, S., Å. N. Austin, U. Bergström, B. K. Eriksson, J. P. Hansen, P. Jacobson, G. Sundblad, M. van Regteren, and J. S. Eklöf. ‘A Cross-Scale Trophic Cascade from Large Predatory Fish to Algae in Coastal Ecosystems’. *Proceedings of the Royal Society B: Biological Sciences* 284, no. 1859 (19 July 2017): 20170045. <https://doi.org/10.1098/rspb.2017.0045>.
- Dore, Mohammed H. I. ‘Climate Change and Changes in Global Precipitation Patterns: What Do We Know?’ *Environment International* 31, no. 8 (1 October 2005): 1167–81. <https://doi.org/10.1016/j.envint.2005.03.004>.
- Eddy, Tyler D., Joey R. Bernhardt, Julia L. Blanchard, William W. L. Cheung, Mathieu Colléter, Hubert du Pontavice, Elizabeth A. Fulton, et al. ‘Energy Flow Through Marine Ecosystems: Confronting Transfer Efficiency’. *Trends in Ecology &*

- Evolution* 36, no. 1 (1 January 2021): 76–86. <https://doi.org/10.1016/j.tree.2020.09.006>.
- EPA, U.S. Environmental Protection Agency (2025) Radionuclide basics: Cesium-137. <https://www.epa.gov/radiation/radionuclide-basics-cesium-137> accessed 16.4.2025
- Eriksson, M., Ikaheimonen, T., Jakobson, E., Nielsen, S. P., Kämäräinen, M., Lüning, M., Aust, M.-O., Osvath, L., Schmied, S., Vilimaite-Silobritiene, B., Suplinska, M., Zalewska, T., & Vartti, V.-P. (2018). *Thematic Assessment of Radioactive Substances in the Baltic Sea, 2011-2015*. Helsinki Commission. Baltic Marine Environment Protection Commission. Baltic Sea Environment Proceedings No. 151
- Essential fish habitats in the Baltic Sea – Identification of potential spawning, recruitment and nursery areas. HELCOM (2021)
- Figueroa, D., O. F. Rowe, J. Paczkowska, C. Legrand, and A. Andersson. ‘Allochthonous Carbon—a Major Driver of Bacterioplankton Production in the Subarctic Northern Baltic Sea’. *Microbial Ecology* 71, no. 4 (1 May 2016): 789–801. <https://doi.org/10.1007/s00248-015-0714-4>.
- Forster, Jack, Andrew G. Hirst, and David Atkinson. ‘Warming-Induced Reductions in Body Size Are Greater in Aquatic than Terrestrial Species’. *Proceedings of the National Academy of Sciences* 109, no. 47 (20 November 2012): 19310–14. <https://doi.org/10.1073/pnas.1210460109>.
- Frigstad, Helene, Guri S. Andersen, Hilde C. Trannum, Maeve McGovern, Lars-Johan Naustvoll, Øyvind Kaste, Anne Deininger, and Dag Ø. Hjermann. ‘Three Decades of Change in the Skagerrak Coastal Ecosystem, Shaped by Eutrophication and Coastal Darkening’. *Estuarine, Coastal and Shelf Science* 283 (5 April 2023): 108193. <https://doi.org/10.1016/j.ecss.2022.108193>.
- Fujii, Manabu, Keisuke Ono, Chihiro Yoshimura, and Manami Miyamoto. ‘The Role of Autochthonous Organic Matter in Radioactive Cesium Accumulation to Riverine Fine Sediments’. *Water Research* 137 (15 June 2018): 18–27. <https://doi.org/10.1016/j.watres.2018.02.063>.
- Fujino, Takeshi, Shota Kobori, Takeshi Nomoto, Masaru Sakai, and Takashi Gomi. ‘Radioactive Cesium Contamination and Its Biological Half-Life in Larvae of *Stenopsyche marmorata* (Trichoptera: Stenopsychidae).’ *Landscape and Ecological Engineering* 14, no. 1 (2018): 37–43. <https://doi.org/10.1007/s11355-017-0339-5>.
- Garnier, Aurélie, Örjan Östman, Jenny Ask, Jingyao Niu, Justine Roth, and Magnus Huss. ‘Water Darkening Modulates the Efficiency of Coastal Eutrophication Mitigation in a Mesocosm Experiment.’ *Canadian Journal of Fisheries and Aquatic Sciences*, ahead of print, NRC Research Press, November 12, 2025. <https://doi.org/10.1139/cjfas-2024-0418>.

- Garzke, J., Connor, S. J., Sommer, U., & O'Connor, M. I. (2019). Trophic interactions modify the temperature dependence of community biomass and ecosystem function. *PLOS Biology*, 17(6), e2006806. <https://doi.org/10.1371/journal.pbio.2006806>
- Gasol, Josep M., Paul A. del Giorgio, and Carlos M. Duarte. 'Biomass Distribution in Marine Planktonic Communities'. *Limnology and Oceanography* 42, no. 6 (1997): 1353–63. <https://doi.org/10.4319/lo.1997.42.6.1353>.
- Gomi, Takashi, Masaru Sakai, Md. Enamul Haque, Kosuke Hosoda, and Hiroto Toda. "Evaluating ¹³⁷Cs Detachment from Coniferous Needle Litter in a Headwater Stream: A Litter Bag Field Experiment." *Landscape and Ecological Engineering* 14, no. 1 (2018): 17–27. <https://doi.org/10.1007/s11355-017-0337-7>.
- Guthrie, D. M. 'Role of Vision in Fish Behaviour'. In *The Behaviour of Teleost Fishes*, edited by Tony J. Pitcher, 75–113. Boston, MA: Springer US, 1986. https://doi.org/10.1007/978-1-4684-8261-4_4.
- Häder, Donat-P., Virginia E. Villafañe, and E. Walter Helbling. 'Productivity of Aquatic Primary Producers under Global Climate Change'. *Photochemical & Photobiological Sciences* 13, no. 10 (17 September 2014): 1370–92. <https://doi.org/10.1039/C3PP50418B>.
- Hampton, Stephanie, Steven Fradkin, Peter Leavitt, and Elizabeth Rosenberger. 'Disproportionate Importance of Nearshore Habitat for the Food Web of a Deep Oligotrophic Lake'. *Marine and Freshwater Research* 62 (28 April 2011): 350–58. <https://doi.org/10.1071/MF10229>.
- Harvey, E. Therese, Susanne Kratzer, and Agneta Andersson. 'Relationships between Colored Dissolved Organic Matter and Dissolved Organic Carbon in Different Coastal Gradients of the Baltic Sea'. *AMBIO* 44, no. 3 (1 June 2015): 392–401. <https://doi.org/10.1007/s13280-015-0658-4>.
- Hačje, Vanessa, Manmohan Sarin, Sylvia G. Sander, Dario Omanović, Purvaja Ramachandran, Christoph Völker, Ricardo O. Barra, and Alessandro Tagliabue. 'Emergent Interactive Effects of Climate Change and Contaminants in Coastal and Ocean Ecosystems'. *Frontiers in Marine Science* 9 (25 July 2022). <https://doi.org/10.3389/fmars.2022.936109>.
- Hayashi, Seiji, Hideki Tsuji, and Ishii Yumiko. 'Effects of Forest Litter on Dissolved ¹³⁷Cs Concentrations in a Highly Contaminated Mountain River in Fukushima'. *Journal of Hydrology: Regional Studies* 41 (1 June 2022): 101099. <https://doi.org/10.1016/j.ejrh.2022.101099>.
- Hecht, T., and C.D. van der Lingen. 'Turbidity-Induced Changes in Feeding Strategies of Fish in Estuaries'. *South African Journal of Zoology* 27, no. 3 (1 January 1992): 95–107. <https://doi.org/10.1080/02541858.1992.11448269>.
- HELCOM (2013): Thematic assessment of long-term changes in radioactivity in the Baltic Sea, 2007-2010. Balt. Sea Environ. Proc. No. 135

- HELCOM (2023): HELCOM activities report for the year 2023. Baltic Sea Environment Proceedings No. 196 <https://helcom.fi/wp-content/uploads/2024/06/Annual-report-2023.pdf>
- HELCOM (2023): State of the Baltic Sea. Third HELCOM holistic assessment 2016-2021. Baltic Sea Environment Proceedings n°194.
- HELCOM. Analysis of total nitrogen in the Baltic Sea and implications for time lag in achieving good environmental status (GES). HELCOM ACTION (2021)
- Heldal, Hilde Elise, Lars Føyn, and Per Varskog. ‘Bioaccumulation of 137Cs in Pelagic Food Webs in the Norwegian and Barents Seas’. *Journal of Environmental Radioactivity* 65, no. 2 (1 January 2003): 177–85. [https://doi.org/10.1016/S0265-931X\(02\)00095-4](https://doi.org/10.1016/S0265-931X(02)00095-4).
- Henseler, Christina, Marie C. Nordström, Anna Törnroos, Martin Snickars, Laurene Pecuchet, Martin Lindegren, and Erik Bonsdorff. ‘Coastal Habitats and Their Importance for the Diversity of Benthic Communities: A Species- and Trait-Based Approach’. *Estuarine, Coastal and Shelf Science* 226 (15 October 2019): 106272. <https://doi.org/10.1016/j.ecss.2019.106272>.
- Horppila, Jukka, Leena Nurminen, Salla Rajala, and Satu Estlander. ‘The Effect of Water Colour on Fish Communities in Boreal Lakes’. *Ecosystems* 28, no. 1 (3 January 2025): 3. <https://doi.org/10.1007/s10021-024-00954-5>.
- Huss, Magnus, Max Lindmark, Philip Jacobson, Renee M. van Dorst, and Anna Gårdmark. ‘Experimental Evidence of Gradual Size-Dependent Shifts in Body Size and Growth of Fish in Response to Warming’. *Global Change Biology* 25, no. 7 (2019): 2285–95. <https://doi.org/10.1111/gcb.14637>.
- IAEA. *Sediment Distribution Coefficients and Concentration Factors for Biota in the Marine Environment*. Technical Reports Series No. 422. International Atomic Energy Agency. Vienna (2004).
- Ikäheimonen, Tarja Katri, Iisa Outola, Vesa-Pekka Vartti, and Pekka Kotilainen. ‘Radioactivity in the Baltic Sea: Inventories and Temporal Trends of 137Cs and 90Sr in Water and Sediments’. *Journal of Radioanalytical and Nuclear Chemistry* 282, no. 2 (1 November 2009): 419–25. <https://doi.org/10.1007/s10967-009-0144-1>.
- Ikpewe, Idongesit E., Alan R. Baudron, Aurore Ponchon, and Paul G. Fernandes. ‘Bigger Juveniles and Smaller Adults: Changes in Fish Size Correlate with Warming Seas’. *Journal of Applied Ecology* 58, no. 4 (2021): 847–56. <https://doi.org/10.1111/1365-2664.13807>.
- Isaksson, Mats, and Bengt Erlandsson. “Models for the Vertical Migration of 137Cs in the Ground — a Field Study.” *Journal of Environmental Radioactivity* 41, no. 2 (1998): 163–82. [https://doi.org/10.1016/S0265-931X\(98\)00004-6](https://doi.org/10.1016/S0265-931X(98)00004-6).
- Iwagami, Sho, Maki Tsujimura, Yuichi Onda, Ryohei Konuma, Yutaro Satou, Koichi Sakakibara, and Vasyl Yoschenko. ‘Dissolved 137Cs Concentrations in Stream Water and Subsurface Water in a Forested Headwater Catchment after the

- Fukushima Dai-Ichi Nuclear Power Plant Accident'. *Journal of Hydrology* 573 (1 June 2019): 688–96. <https://doi.org/10.1016/j.jhydrol.2019.04.019>.
- Jansson, Mats, Lennart Persson, André M. De Roos, Roger I. Jones, and Lars J. Tranvik. 'Terrestrial Carbon and Intraspecific Size-Variation Shape Lake Ecosystems'. *Trends in Ecology & Evolution* 22, no. 6 (1 June 2007): 316–22. <https://doi.org/10.1016/j.tree.2007.02.015>.
- Jennings, Simon, and Kate Collingridge. 'Predicting Consumer Biomass, Size-Structure, Production, Catch Potential, Responses to Fishing and Associated Uncertainties in the World's Marine Ecosystems'. *PLOS ONE* 10, no. 7 (30 July 2015): e0133794. <https://doi.org/10.1371/journal.pone.0133794>.
- Karlsson, Jan, Ann-Kristin Bergström, Pär Byström, Cristian Gudasz, Patricia Rodríguez, and Catherine Hein. 'Terrestrial Organic Matter Input Suppresses Biomass Production in Lake Ecosystems'. *Ecology* 96, no. 11 (2015): 2870–76. <https://doi.org/10.1890/15-0515.1>.
- Karlsson, Jan, Pär Byström, Jenny Ask, Per Ask, Lennart Persson, and Mats Jansson. 'Light Limitation of Nutrient-Poor Lake Ecosystems'. *Nature* 460, no. 7254 (July 2009): 506–9. <https://doi.org/10.1038/nature08179>.
- Knapinska-Skiba, D., R. Bojanowski, and R. Piękoś. "Activity Concentration of Caesium-137 in Seawater and Plankton of the Pomeranian Bay (the Southern Baltic Sea) before and after Flood in 1997." *Marine Pollution Bulletin* 46, no. 12 (2003): 1558–62. [https://doi.org/10.1016/S0025-326X\(03\)00317-5](https://doi.org/10.1016/S0025-326X(03)00317-5).
- Larsen, Søren, Tom Andersen, and Dag O. Hessen. 'Climate Change Predicted to Cause Severe Increase of Organic Carbon in Lakes'. *Global Change Biology* 17, no. 2 (2011): 1186–92. <https://doi.org/10.1111/j.1365-2486.2010.02257.x>.
- Legendre, Louis, and Fereidoun Rassoulzadegan. 'Plankton and Nutrient Dynamics in Marine Waters'. *Ophelia* 41, no. 1 (1 February 1995): 153–72. <https://doi.org/10.1080/00785236.1995.10422042>.
- Lestaevel, P., R. Racine, H. Bensoussan, C. Rouas, Y. Gueguen, I. Dublineau, J. -M. Bertho, P. Gourmelon, J. -R. Jourdain, and M. Souidi. 'Césium 137 : Propriétés et Effets Biologiques Après Contamination Interne'. *Médecine Nucléaire* 34, no. 2 (1 February 2010): 108–18. <https://doi.org/10.1016/j.mednuc.2009.12.003>.
- Lindeman. "The Trophic-Dynamic Aspect of Ecology (1942) Ecology - Wiley Online Library." <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1930126>.
- Lindmark, Max, Asta Audzijonyte, Julia L. Blanchard, and Anna Gårdmark. 'Temperature Impacts on Fish Physiology and Resource Abundance Lead to Faster Growth but Smaller Fish Sizes and Yields under Warming'. *Global Change Biology* 28, no. 21 (2022): 6239–53. <https://doi.org/10.1111/gcb.16341>.
- Lindmark, Max, Jan Ohlberger, and Anna Gårdmark. 'Optimum Growth Temperature Declines with Body Size within Fish Species'. *Global Change Biology* 28, no. 7 (2022): 2259–71. <https://doi.org/10.1111/gcb.16067>.

- Lindmark, Max, Magnus Huss, Jan Ohlberger, and Anna Gårdmark. ‘Temperature-Dependent Body Size Effects Determine Population Responses to Climate Warming’. *Ecology Letters* 21, no. 2 (2018): 181–89. <https://doi.org/10.1111/ele.12880>.
- Lindmark, Max, Malin Karlsson, and Anna Gårdmark. ‘Larger but Younger Fish When Growth Outpaces Mortality in Heated Ecosystem’. Edited by David A Donoso, Meredith C Schuman, and Christine Stawitz. *eLife* 12 (9 May 2023): e82996. <https://doi.org/10.7554/eLife.82996>.
- Mehner, T., Attermeyer, K., Brauns, M., Brothers, S., Hilt, S., Scharnweber, K., van Dorst, R. M., Vanni, M. J., & Gaedke, U. (2022). Trophic Transfer Efficiency in Lakes. *Ecosystems*, 25(8), 1628–1652. <https://doi.org/10.1007/s10021-022-00776-3>
- Mirzoeva, Natalia, Nickolai Shadrin, Svetlana Arkhipova, Oksana Miroshnichenko, Natalia Kravchenko, and Elena Anufrieva. ‘Does Salinity Affect the Distribution of the Artificial Radionuclides 90Sr and 137Cs in Water of the Saline Lakes? A Case of the Crimean Peninsula’. *Water* 12, no. 2 (February 2020): 349. <https://doi.org/10.3390/w12020349>.
- Mooney, Benjamin Paul, Anna Gårdmark, Carolyn Faithfull, Renee Mina van Dorst, and Magnus Huss. “Warmer Lakes Support Phytoplankton Over Fish.” *Global Change Biology* 31, no. 6 (2025): e70288. <https://doi.org/10.1111/gcb.70288>.
- Nair, Satish. “Chapter 23 - Understanding the Risks of Ionizing Radiation Exposure: A Case of Dichotomy between Science and Policy.” In *Biological and Environmental Hazards, Risks, and Disasters (Second Edition)*, edited by Ramesh Sivanpillai and John F. Shroder. Hazards and Disasters Series. Elsevier, 2023. <https://doi.org/10.1016/B978-0-12-820509-9.00015-0>.
- Nakahara, M., T. Koyanagi, and M. Saiki. ‘Temperature Effect on the Concentration of Radionuclides by Marine Organisms’. *Journal of Radiation Research* 18, no. 2 (1 May 1977): 122–31. <https://doi.org/10.1269/jrr.18.122>.
- Niu, Jingyao, Magnus Huss, Anti Vasemägi, and Anna Gårdmark. “Decades of Warming Alters Maturation and Reproductive Investment in Fish.” *Ecosphere* 14, no. 1 (2023): e4381. <https://doi.org/10.1002/ecs2.4381>.
- Norman, Sven, Karin A. Nilsson, Marcus Klaus, David Seekell, Jan Karlsson, and Pär Byström. ‘Effects of Habitat-Specific Primary Production on Fish Size, Biomass, and Production in Northern Oligotrophic Lakes’. *Ecosystems* 25, no. 7 (November 2022): 1555–70. <https://doi.org/10.1007/s10021-021-00733-6>.
- Nunes, M., & Leston, S. (2020). Coastal pollution: an overview. *Life Below Water*, 1–11.
- O’Connor, Mary I. ‘Warming Strengthens an Herbivore–Plant Interaction’. *Ecology* 90, no. 2 (2009): 388–98. <https://doi.org/10.1890/08-0034.1>.
- Opdal, Anders Frugård, Tom Andersen, Dag O. Hessen, Christian Lindemann, and Dag L. Aksnes. ‘Tracking Freshwater Browning and Coastal Water Darkening from

- Boreal Forests to the Arctic Ocean'. *Limnology and Oceanography Letters* 8, no. 4 (2023): 611–19. <https://doi.org/10.1002/lol2.10320>.
- Pauly, Daniel, and Villy Christensen. 'Pauly, D. & Christensen, V. Primary Production Required to Sustain Global Fisheries. Nature 374, 255-257'. *Nature* 374 (16 March 1995). <https://doi.org/10.1038/374255a0>.
- Periáñez, R., R. Bezhenar, I. Brovchenko, et al. "Marine Radionuclide Transport Modelling: Recent Developments, Problems and Challenges." *Environmental Modelling & Software* 122 (December 2019): 104523. <https://doi.org/10.1016/j.envsoft.2019.104523>.
- Roth, Allison M., Vincent Fugère, Marco A. Rodríguez, et al. "Differential Effects of Freshwater Browning across Fish Species: Consequences for Individual- to Community-Level Fish Traits in North Temperate Lakes." *Biological Reviews* n/a, no. n/a (n.d.). <https://doi.org/10.1111/brv.70074>.
- Rowan, David J., Lorna A. Chant, and Joseph B. Rasmussen. 'The Fate of Radiocesium in Freshwater Communities—Why Is Biomagnification Variable Both within and between Species?' *Journal of Environmental Radioactivity* 40, no. 1 (1 July 1998): 15–36. [https://doi.org/10.1016/S0265-931X\(97\)00066-0](https://doi.org/10.1016/S0265-931X(97)00066-0).
- Saiki, M., and T. Koyanagi. 'Temperature Effect on the Concentration of Radionuclides by Marine Organisms'. *Journal of Radiation Research* 18, no. 2 (1977): 122–31. <https://doi.org/10.1269/jrr.18.122>.
- Sand-Jensen, Kaj, and Jens Borum. 'Interactions among Phytoplankton, Periphyton, and Macrophytes in Temperate Freshwaters and Estuaries'. *Aquatic Botany, Ecology of Submersed Aquatic Macrophytes*, 41, no. 1 (1 January 1991): 137–75. [https://doi.org/10.1016/0304-3770\(91\)90042-4](https://doi.org/10.1016/0304-3770(91)90042-4).
- Särkkä, Jukka, Anneli Keskitalo, and Antti Luukko. 'Temporal Changes in Concentration of Radiocaesium in Lake Sediment and Fish of Southern Finland as Related to Environmental Factors'. *Science of The Total Environment* 191, no. 1 (18 November 1996): 125–36. [https://doi.org/10.1016/0048-9697\(96\)05254-0](https://doi.org/10.1016/0048-9697(96)05254-0).
- Solokas, Mary A., Zachary S. Feiner, Robert Al-Chokachy, Phaedra Budy, J. Tyrell DeWeber, Jouko Sarvala, Greg G. Sass, Scott A. Tolentino, Timothy E. Walsworth, and Olaf P. Jensen. 'Shrinking Body Size and Climate Warming: Many Freshwater Salmonids Do Not Follow the Rule'. *Global Change Biology* 29, no. 9 (2023): 2478–92. <https://doi.org/10.1111/gcb.16626>.
- Solomon, Christopher T., Stuart E. Jones, Brian C. Weidel, Ishi Buffam, Megan L. Fork, Jan Karlsson, Søren Larsen, et al. 'Ecosystem Consequences of Changing Inputs of Terrestrial Dissolved Organic Matter to Lakes: Current Knowledge and Future Challenges'. *Ecosystems* 18, no. 3 (1 April 2015): 376–89. <https://doi.org/10.1007/s10021-015-9848-y>.
- Sommer, Ulrich, Herwig Stibor, Alexis Katechakis, Frank Sommer, and Thomas Hansen. 'Pelagic Food Web Configurations at Different Levels of Nutrient Richness and Their Implications for the Ratio Fish Production:Primary

- Production'. *Hydrobiologia* 484, no. 1 (1 September 2002): 11–20. <https://doi.org/10.1023/A:1021340601986>.
- Strupczewski, A. 'Accident Risks in Nuclear-Power Plants'. *Applied Energy*, Energex 2002 - Oil and Gas - Topic III and Nuclear Energy - Topic IV, 75, no. 1 (1 May 2003): 79–86. [https://doi.org/10.1016/S0306-2619\(03\)00021-7](https://doi.org/10.1016/S0306-2619(03)00021-7).
- Sundbom, Marcus, Markus Meili, Evert Andersson, Mikael Östlund, and Anders Broberg. 'Long-Term Dynamics of Chernobyl 137Cs in Freshwater Fish: Quantifying the Effect of Body Size and Trophic Level'. *Journal of Applied Ecology* 40, no. 2 (2003): 228–40. <https://doi.org/10.1046/j.1365-2664.2003.00795.x>.
- Takata, Hyoe. 'Environmental Recovery from 137Cs Contamination in Japanese Coastal Waters Shown by Comparison of Temporal Distributions with European Seas'. *Journal of Environmental Radioactivity* 251–252 (1 October 2022): 106961. <https://doi.org/10.1016/j.jenvrad.2022.106961>.
- Tanaka, S., T. Adati, T. Takahashi, K. Fujiwara, and S. Takahashi. 'Concentrations and Biological Half-Life of Radioactive Cesium in Epigeic Earthworms after the Fukushima Dai-Ichi Nuclear Power Plant Accident'. *Journal of Environmental Radioactivity* 192 (1 December 2018): 227–32. <https://doi.org/10.1016/j.jenvrad.2018.06.020>.
- Thomas, Derin M., and Nicholas S. Fisher. 'Evaluation of Body Size and Temperature on 137Cs Uptake in Marine Animals'. *Journal of Environmental Radioactivity* 202 (1 June 2019): 25–31. <https://doi.org/10.1016/j.jenvrad.2019.02.005>.
- Tsuji, Hideki, Tetsuo Yasutaka, Yoshishige Kawabe, Takeo Onishi, and Takeshi Komai. 'Distribution of Dissolved and Particulate Radiocesium Concentrations along Rivers and the Relations between Radiocesium Concentration and Deposition after the Nuclear Power Plant Accident in Fukushima.' *Water Research* 60 (September 2014): 15–27. <https://doi.org/10.1016/j.watres.2014.04.024>.
- Ullah, Hadayet, Ivan Nagelkerken, Silvan U. Goldenberg, and Damien A. Fordham. 'Climate Change Could Drive Marine Food Web Collapse through Altered Trophic Flows and Cyanobacterial Proliferation'. *PLOS Biology* 16, no. 1 (9 January 2018): e2003446. <https://doi.org/10.1371/journal.pbio.2003446>.
- Uszko, Wojciech, Magnus Huss, and Anna Gårdmark. 'Smaller Species but Larger Stages: Warming Effects on Inter- and Intraspecific Community Size Structure'. *Ecology* 103, no. 7 (2022): e3699. <https://doi.org/10.1002/ecy.3699>.
- Vadeboncoeur, Yvonne, Erik Jeppesen, M. Jake Vander Zanden, Hans-Henrik Schierup, Kirsten Christoffersen, and David M. Lodge. 'From Greenland to Green Lakes: Cultural Eutrophication and the Loss of Benthic Pathways in Lakes'. *Limnology and Oceanography* 48, no. 4 (2003): 1408–18. <https://doi.org/10.4319/lo.2003.48.4.1408>.
- Van Dorst, Renee M., Anna Gårdmark, Richard Svanbäck, and Magnus Huss. 'Zooplanktivore Fish Body Growth Responses to Browning-Induced Light

- Limitation Vary over Ontogeny, but Not with Fish Density'. *Ecology of Freshwater Fish* 31, no. 1 (2022): 17–28. <https://doi.org/10.1111/eff.12605>. Van Dorst, Renee M., Anna Gårdmark, Richard Svanbäck, Ulrika Beier, Gesa A. Weyhenmeyer, and Magnus Huss. 'Warmer and Browner Waters Decrease Fish Biomass Production'. *Global Change Biology* 25, no. 4 (2019): 1395–1408. <https://doi.org/10.1111/gcb.14551>.
- Varela, R., M. de Castro, J. M. Dias, and M. Gómez-Gesteira. 'Coastal Warming under Climate Change: Global, Faster and Heterogeneous'. *Science of The Total Environment* 886 (15 August 2023): 164029. <https://doi.org/10.1016/j.scitotenv.2023.164029>.
- Vasconcelos, Francisco Rivera, Sebastian Diehl, Patricia Rodríguez, Per Hedström, Jan Karlsson, and Pär Byström. 'Asymmetrical Competition between Aquatic Primary Producers in a Warmer and Browner World'. *Ecology* 97, no. 10 (2016): 2580–92. <https://doi.org/10.1002/ecy.1487>.
- Verberk, Wilco C.E.P., David Atkinson, K. Natan Hoefnagel, Andrew G. Hirst, Curtis R. Horne, and Henk Siepel. 'Shrinking Body Sizes in Response to Warming: Explanations for the Temperature–Size Rule with Special Emphasis on the Role of Oxygen'. *Biological Reviews* 96, no. 1 (2021): 247–68. <https://doi.org/10.1111/brv.12653>.
- Vives I Batlle, J., M. Aoyama, C. Bradshaw, et al. "Marine Radioecology after the Fukushima Dai-Ichi Nuclear Accident: Are We Better Positioned to Understand the Impact of Radionuclides in Marine Ecosystems?" *The Science of the Total Environment* 618 (March 2018): 80–92. <https://doi.org/10.1016/j.scitotenv.2017.11.005>.
- Weidel, Brian C., Baglini ,Katherine, Jones ,Stuart E., Kelly ,Patrick T., Solomon ,Christopher T., and Jacob A. and Zwart. 'Light Climate and Dissolved Organic Carbon Concentration Influence Species-Specific Changes in Fish Zooplanktivory'. *Inland Waters* 7, no. 2 (3 April 2017): 210–17. <https://doi.org/10.1080/20442041.2017.1329121>.
- Wikner, Johan, and Agneta Andersson. 'Increased Freshwater Discharge Shifts the Trophic Balance in the Coastal Zone of the Northern Baltic Sea'. *Global Change Biology* 18, no. 8 (2012): 2509–19. <https://doi.org/10.1111/j.1365-2486.2012.02718.x>.
- Yamazaki, Hideo. 'Radioactive Contamination of Fishes in Aquatic Ecosystems'. In *Radioactive Contamination of the Tokyo Metropolitan Area: Five Years after the Fukushima Nuclear Accident*, edited by Hideo Yamazaki, 181–231. Singapore: Springer, 2020. https://doi.org/10.1007/978-981-15-7368-2_8.
- Zalewska, Tamara, and Maria Suplińska. 'Anthropogenic Radionuclides ¹³⁷Cs and ⁹⁰Sr in the Southern Baltic Sea Ecosystem'. *Oceanologia* 55, no. 3 (1 August 2013): 485–517. <https://doi.org/10.5697/oc.55-3.485>.