

Methylmercury

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Abstract

Methylmercury (MeHg) is the biomagnified organometallic form of mercury that dominates dietary exposure in populations consuming fish. Methylmercury is a known developmental neurotoxicant; the literature on fetal and early-childhood exposure is extensive and forms the basis of advisories in most jurisdictions. Large predatory fish (shark, swordfish, king mackerel, bigeye tuna, tilefish) and marine mammals are the principal food-system sources. The distinction between methylmercury and total mercury is maintained throughout this wiki because methylmercury drives the health interpretation in dietary contexts; see mercury, total for the companion page.

1 | Overview

Ufelle & Barchowsky 2021 supports this species page with textbook-level context on aquatic methylation, biomagnification, gastrointestinal absorption, blood-brain-barrier and placental transfer, fecal elimination, neurotoxicity, and treatment strategies that interrupt enterohepatic cycling. It is a toxicology source, not a food occurrence dataset.

2 | Toxicology

Methylmercury crosses the blood-brain barrier and the placenta. Fetal exposure during gestation produces developmental neurotoxicity at levels well below those that produce overt symptoms in adults; the historical reference cohorts in the Faroe Islands and Seychelles establish the developmental-exposure dose-response that anchors most regulatory advisories. Adult toxicity manifests as paresthesia, ataxia, visual-field constriction, and dysarthria; the threshold for chronic adult symptoms is substantially higher than the threshold for prenatal effects. Hair-mercury serves as a long-term biomarker of methylmercury exposure because methylmercury binds preferentially to cysteine residues in keratin.

Cardiovascular effects of methylmercury exposure are an active area of research; some cohort studies report associations between methylmercury exposure and cardiovascular endpoints, while others do not. The wiki

does not yet take a synthesis position on cardiovascular MeHg endpoints pending dedicated ingest of the cardiovascular evidence base. See Ufelle & Barchowsky 2021 for the textbook-level toxicology context.

3 | Dietary exposure routes

Methylmercury exposure in non-occupational populations is dominated by fish consumption. The hierarchy of MeHg concentration follows trophic level: large long-lived predatory fish (shark, swordfish, king mackerel, tilefish from the Gulf of Mexico, bigeye tuna) carry the highest MeHg loads because they bioaccumulate the metal over their lifespan from prey already carrying methylmercury. Smaller short-lived fin-fish (sardines, anchovies, herring, salmon, trout, tilapia) carry substantially less. Shellfish carry less methylmercury than fin-fish of similar size because of lower trophic position and shorter lifespan. Marine mammals (whales, seals) are exposed populations where they are part of the diet (subsistence fishing communities, indigenous diets), and the MeHg loads in these matrices are among the highest documented in any human-consumed food.

For per-species detail and the trophic-level rationale, see fish, freshwater fish, shark, and canned tuna. For the regulatory side, see the FDA methylmercury action level (1.0 ppm in fish, fda-methylmercury-fish-1-ppm when added) and the EU Reg. 2023/915 Hg maximum levels for fishery products.

4 | Regulatory and advisory framework

Regulatory instruments for methylmercury split into three classes. Maximum levels in food (binding) include the EU Reg. 2023/915 species-specific Hg maximum levels for fishery products (which the EU applies as total Hg with species-specific thresholds, on the assumption that the vast majority of mercury in fishery matrices is methylmercury) and Codex methylmercury maximum levels for fish. Action levels (nonbinding but enforcement--relevant) include the FDA action level of 1.0 ppm methylmercury in fish, established before methylmercury speciation testing was routine and applied as a total-mercury proxy in many contexts. Consumption advisories (nonbinding consumer guidance) include the FDA/EPA joint advice on fish consumption for pregnant women, women of childbearing age, and young children, which categorizes fish into best-choice, good-choice, and avoid tiers.

The Heavy Metal Index records methylmercury limits and total-mercury limits as separate values per the methodology speciation rule even when a regulatory instrument permits the total-Hg proxy. Where a source reports tHg in a matrix where MeHg dominates (most fin-fish, most shellfish), the value is admitted as MeHg-context evidence; where the source reports tHg in a matrix where inorganic Hg dominates (rice, some grains, some animal organs), the value is admitted as tHg evidence only and is not used as MeHg evidence.

5 | Vulnerable populations

The dose-response between methylmercury exposure and developmental neurotoxicity makes the fetus, the breastfed infant, and the young child the principal at-risk populations. The FDA/EPA fish-consumption advisory targets pregnant women and women of childbearing age specifically because in-utero exposure is the most consequential exposure window. Frequent fish consumers (subsistence-fishing communities, sport-fishing populations targeting predatory fish, populations whose cultural diet includes marine mammals) are the populations whose chronic intake can approach or exceed the JECFA Provisional Tolerable Weekly Intake even when consuming "safe-tier" fish in normal serving sizes.

6 | Microbiome

Gut microbiota influence methylmercury bioavailability through both methylation and demethylation activity in the intestinal lumen. The microbiome-MeHg interaction is an active research area; mechanism-level evidence is being routed to methylmercury-microbiome (pending) and the WikiBiome crosswalk is targeted for this material once the ingest reaches density.

7 | Climate-driven enhancement of MeHg production

Climate change is reshaping MeHg production dynamics in freshwater systems. Wu et al. 2025 (PNAS) compiled approximately 13,000 fish mercury samples across 164 sampling sites in China spanning 2005 to 2020 and combined machine learning with climate scenario modeling to project MeHg concentrations in freshwater wild fish. Under both SSP2-4.5 and SSP5-8.5 pathways, national average MeHg in freshwater wild fish is projected to rise by approximately 60 percent by 2031 to 2060.

The dominant individual climate driver is increased solar radiation (approximately 53 percent contribution), which the authors attribute to enhanced photochemical methylation in aquatic systems. Maximum temperature exerts a negative influence in the far future (after 2070) under the high-emissions pathway, but the 2031 to 2060 window is dominated by the solar radiation channel. The mechanism, climate-driven enhancement of microbial and photochemical methylation, is not specific to China; it operates through fundamental aquatic biogeochemistry. However, the model is parameterized on Chinese data, and independent confirmation from non-Chinese watersheds would strengthen the projection substantially.

The present-day baseline from the same dataset establishes that freshwater wild fish carry MeHg concentrations 2.9 to 6.2 times higher than freshwater farmed fish across trophic classes, and 1.7 times higher than marine wild fish in the same trophic class. Mean MeHg in freshwater wild fish of typical adult size (40 ± 5 cm body length) was $30.9 \mu\text{g/kg}$ wet weight. Freshwater fish consumption accounted for 51 percent of China's total fish MeHg intake in 2011.

A consequence of this trend is that MeHg thresholds and fish-consumption advisories calibrated against historical fish Hg data are drawing on a baseline that is actively shifting. See climate-metals-tradeoffs for the convergent analysis with rice irrigation trade-offs, and subsistence-fishing-mehg-disparity for the equity dimension.

8 | Biogeochemical mechanism of MeHg production

MeHg is produced from inorganic mercury (Hg^{2+}) primarily by microbial methylation in anoxic environments: wetland sediments, peatlands, paddy soils, lake hypolimnia, and the digestive tracts of sediment-feeding invertebrates. The dominant methylating microorganisms are sulfate-reducing bacteria, iron-reducing bacteria, and certain methanogenic archaea, all of which encode the *hgcA* / *hgcB* gene pair that catalyzes the Hg^{2+} -to-MeHg conversion. Seelen et al. 2023 (Nature Communications) demonstrates that dissolved organic matter thiol concentrations control MeHg bioavailability across the terrestrial-marine aquatic continuum — thiols compete with cellular uptake systems for Hg-binding, so high-thiol waters reduce MeHg bioaccumulation efficiency, while low-thiol systems amplify it.

Counteracting demethylation pathways operate in parallel. Photochemical demethylation in surface waters (UV-A and UV-B driven, peaking in clear oligotrophic lakes) removes MeHg from the water column. Microbial demethylation by mercury-resistant bacteria carrying the *mer* operon (encoding MerB and MerA) cleaves the C-Hg bond and reduces inorganic Hg^{2+} to volatile Hg^0 . Net MeHg accumulation in any system depends on

the balance: high methylation rate plus low demethylation rate plus high bioavailability equals high biota MeHg burden.

Zhou et al. 2025 (Nature Communications) demonstrates that microbial communities in Chinese paddy soils can actively mitigate MeHg accumulation in rice when methylation-suppressing taxa are present, suggesting future microbiome-engineering approaches to rice MeHg control. Cui et al. 2022 models MeHg distribution across 464,368 1-km² Chinese rice paddy grids and shows tight coupling between paddy water management, sediment Hg burden, and rice-grain MeHg. Sonke et al. 2023 synthesizes the global Hg biogeochemistry context: legacy emissions from coal combustion, artisanal gold mining, and industrial sources are the primary anthropogenic Hg loading into watersheds, with atmospheric deposition the dominant transport pathway to remote receiving systems.

A consequence for food-system exposure is that MeHg burden in any food commodity reflects upstream biogeochemistry that operates over decades-to-centuries timescales. Even if Hg emissions stopped tomorrow, the legacy Hg already in watershed sediments and oceans would continue producing MeHg for decades. Per Dietz et al. 2025 isotope-based source attribution, ocean-transported legacy Hg drives Arctic food web MeHg even where local emissions are negligible.

9 | Biomagnification and the trophic-level rule

MeHg biomagnifies through aquatic food webs at characteristic rates that are remarkably consistent across systems. Per-trophic-level magnification factors (MeHg concentration in predator / MeHg concentration in prey) typically range 3 to 10×; over a 4-trophic-level food chain (algae → zooplankton → small fish → predatory fish), the cumulative magnification produces MeHg concentrations in apex predators 100 to 10,000× higher than the dissolved water-column MeHg. Hall et al. 2023 documents this in tidal marsh food webs across four marsh features and three site categories.

The trophic-level dependence is why fish-species selection is the dominant lever for reducing dietary MeHg exposure (see seafood and fresh-fish Levers sections). Atmospheric Hg deposition is largely unaffected by individual consumer choices; trophic-level positioning of the species consumed is the variable consumers and certifiers can shift. Li et al. 2024 (PNAS) models global fisheries to estimate catch-weighted MeHg concentrations for 1,774 marine species and demonstrates that global fishing patterns systematically expose human populations to high-MeHg apex predators because fisheries economics favor large, long-lived species.

10 | Selenium-mercury antagonism

Selenium (Se) and mercury share a high binding affinity (Hg-Se bond formation energy approximately 70 kcal/mol, among the strongest in biochemistry). The Selenium Health Benefit Value (HBV) framework, formalized by Ralston et al. 2014, proposes that the Se:Hg molar ratio in a consumed seafood determines whether Se is bioavailable to support selenoprotein synthesis after Hg-Se binding, or whether Hg sequesters all dietary Se as inert HgSe particles. When molar Se exceeds molar Hg in the consumed matrix, net Se is bioavailable and selenoprotein-mediated antioxidant defenses (glutathione peroxidase, thioredoxin reductase, iodothyronine deiodinases) remain functional; when molar Hg exceeds molar Se, Hg-Se sequestration depletes Se from selenoprotein synthesis and the secondary cascade — oxidative stress, thyroid disruption, peroxidative tissue damage — drives the toxicological endpoint as much as direct MeHg neurotoxicity does.

Most fin-fish and shellfish have Se:Hg molar ratios above 1 (Se in excess); the notable exception is large predatory fish (swordfish, mako shark, marlin) where Hg can exceed Se. Chamorro et al. 2024 documents Se:Hg

above 1 in most Atlantic bluefin tuna samples despite high absolute Hg burden, interpreted as net selenium bioavailability that may partially mitigate MeHg neurotoxicity. The mechanism is consistent with experimental data but quantitative risk modulation has not yet been established. The Se:Hg framework is therefore best treated as an explanatory factor for differential cohort sensitivity, and the literature does not support relaxing MeHg ceilings on Se-rich species on the basis of this mechanism alone.

11 | Faroe Islands and Seychelles cohort dose-response

Two long-running prospective birth cohort studies, the Faroe Islands cohort (initiated 1986, with follow-up through young adulthood) and the Seychelles Child Development Study (initiated 1989), provide the foundational dose-response data for MeHg developmental neurotoxicity that anchors most regulatory advisory derivation.

The Faroe Islands cohort, where dietary Hg exposure comes primarily from pilot whale consumption (very high MeHg, often >2 mg/kg in muscle), found consistent associations between cord-blood mercury and child neurodevelopmental endpoints at ages 7 and 14 (verbal/visuospatial/memory deficits at maternal-hair Hg around 10 µg/g, corresponding to fetal blood Hg around 40 µg/L). The Seychelles cohort, where dietary Hg exposure comes from ocean fish consumption (~12 fish meals per week, mean maternal-hair Hg around 6-7 µg/g), found no comparable adverse associations after extensive follow-up.

The interpretation framework: the two cohorts differ in exposure source (whale vs ocean fish), nutrient co-exposure profile (Faroese whale carries less of the long-chain omega-3 polyunsaturated fatty acids that may protect neurodevelopment; ocean fish carries more), and possibly selenium co-exposure (Se:Hg in pilot whale vs ocean fish). The current EFSA TWI of 1.3 µg/kg bw/week is calibrated against the Faroe cohort dose-response; the JECFA PTWI of 1.6 µg/kg bw/week reflects a less-conservative interpretation. (EFSA set a definitive tolerable weekly intake in 2012; the "provisional" designation is JECFA's.) EPA's IRIS RfD of 0.1 µg/kg bw/day (=0.7 µg/kg bw/week, the most conservative of the three) reflects an additional uncertainty factor applied to the Faroe data. See EFSA 2012, JECFA 2004, and EPA IRIS 2001 for the regulatory derivation details.

12 | Polyunsaturated fatty acid (PUFA) modulation of MeHg risk

The same fish-consumption pattern that delivers MeHg also delivers long-chain omega-3 polyunsaturated fatty acids (EPA, DHA, docosapentaenoic acid). These PUFAs support fetal neurodevelopment through membrane phospholipid composition, neuronal differentiation, and anti-inflammatory eicosanoid signaling. The net risk-benefit balance for fish consumption during pregnancy depends on the MeHg/PUFA ratio of the consumed species: high in apex predators (high MeHg, modest PUFA) versus low in small oily fish (modest MeHg, high PUFA).

Vejrup et al. 2022 (Norwegian Mother, Father and Child Cohort, n=51,238 mother-child pairs) finds that prenatal MeHg exposure from fish intake associates with child emotional and behavioral problems at certain MeHg levels, but the association is attenuated when fish intake is decomposed into species categories with different PUFA content. McSorley et al. 2020 (Seychelles cohort follow-up at age 19) finds that both MeHg and long-chain PUFA associate with immune endpoints, with PUFA showing potentially protective effects that complicate any single-marker interpretation.

A MeHg ceiling on its own is therefore not the complete picture. Substitution from tuna toward small oily fish (sardine, anchovy, herring, mackerel) delivers a double benefit in the literature: lower MeHg and higher PUFA. This is why the evidence supports species-level guidance rather than a single uniform MeHg cap applied equally across all fish.

13 | Biomarkers and exposure assessment

Three biomarkers anchor MeHg exposure assessment, each with different exposure-window sensitivity and analytical method:

- **Hair mercury (total Hg by ICP-MS or CV-AAS after acid digestion).** Reflects systemic MeHg exposure over the 2-3 months preceding the hair-sample collection window. Hair Hg is approximately 250× the simultaneous whole-blood Hg concentration because of preferential MeHg binding to cysteine residues in keratin. Used for cohort epidemiology (Faroe, Seychelles), occupational surveillance, and population-monitoring programs. Cegolon et al. 2022 and Oliveira et al. 2022 are recent applications.
- **Whole blood mercury (total Hg by ICP-MS or CV-AFS).** Reflects recent (days-to-weeks) MeHg exposure. Used clinically for acute/recent exposure assessment and in pregnancy monitoring where cord blood is the gold-standard fetal-exposure indicator.
- **Urine mercury.** Reflects inorganic mercury exposure primarily, not MeHg (MeHg is excreted predominantly in feces). Used for occupational dental and chlor-alkali exposure assessment, not MeHg.

Martinez-Morata et al. 2023 is the current state-of-the-science review on metal biomarkers for exposure assessment. Hair mercury is the best-validated biomarker for population-level intake assessment, reflecting integrated exposure over the preceding 2-3 months; whole blood is appropriate for acute-exposure investigation, reflecting recent days-to-weeks exposure.

14 | Analytical methods for MeHg in food

Mercury speciation methods separate MeHg from inorganic Hg before quantification:

- **Cold vapor atomic fluorescence spectrometry (CV-AFS).** Total Hg quantification after acid digestion; the dominant routine method for total mercury. Used for tHg-as-proxy when MeHg/tHg ratios are well-characterized (most fin-fish at 80-95% MeHg per BfR 2024).
- **Thermal decomposition amalgamation AAS (TDA-AAS, e.g., DMA-80, LECO AMA-254).** Direct total Hg quantification in solid samples without prior digestion. Method of choice for rapid throughput in finfish monitoring. Carter et al. 2025 documents FDA method validation for combined TDA-AAS plus SALLE extraction for both MeHg and total Hg in finfish.
- **Gas chromatography ICP-MS (GC-ICP-MS) and liquid chromatography ICP-MS (LC-ICP-MS).** Direct MeHg quantification after derivatization or extraction. The reference methods for MeHg speciation in regulatory and certification contexts.
- **Isotope-dilution MS.** Highest-accuracy MeHg quantification for reference-material certification and trace-level work.

On the analytical hierarchy: tHg by TDA-AAS is a sound proxy for routine lot-level screening on finfish, where MeHg accounts for 80-95 percent of total Hg; speciated MeHg by GC-ICP-MS or LC-ICP-MS is required wherever a measurement must explicitly distinguish MeHg from total Hg, including any threshold work that differentiates lower-trophic species from apex predators.

15 | Rice as a secondary MeHg exposure pathway

Rice is the second-most-important dietary MeHg source after fish, particularly in Asian populations with low fish consumption but high paddy-grown rice consumption. Paddy rice grown in contaminated soils (artisanal--gold-mining-impacted watersheds, chlor-alkali-contaminated regions, peatland-overlying paddies with high sulfate-reducing bacterial activity) can carry MeHg in the 5-50 µg/kg range, with extreme cases exceeding 100 µg/kg.

Brombach et al. 2016 reports that MeHg in commercial European rice varies more than one order of magnitude across products, with country of origin (rice from regions with documented sediment Hg burden carrying more MeHg) as the primary explanatory variable. Cui et al. 2022 models MeHg in Chinese paddy systems at 1-km² resolution. Rothenberg et al. 2021 documents a cohort in rural China where rice-derived maternal MeHg exposure associates with child neurodevelopmental endpoints — the first cohort study to demonstrate the rice-MeHg pathway as a meaningful contributor to developmental risk independent of the fish pathway.

A consequence for exposure assessment is that populations with high rice intake (especially from at-risk regions) and low fish intake may still have meaningful MeHg exposure that fish-consumption advisories do not address. The wiki's rice-related ingredient pages (rice, rice-cereal, rice-flour) record the MeHg pathway alongside the better-known iAs pathway.

16 | Open questions

Several MeHg-toxicology and -exposure questions remain active research areas where the wiki does not yet take a synthesis position:

- **Cardiovascular MeHg effects.** Some cohort studies report MeHg-cardiovascular associations; others do not. Whether MeHg contributes meaningfully to cardiovascular risk in moderate-intake populations remains contested.
- **Thyroid cancer and MeHg.** Webster et al. 2024 meta-analysis examines this; the evidence base is small but suggestive.
- **Climate-change projection robustness outside China.** Wu et al. 2025 documents +60% MeHg projection by 2031-2060 for Chinese freshwater fish. Whether this generalizes to non-Chinese watersheds depends on parameter transferability that has not been independently validated.
- **Selenium-MeHg quantitative risk modulation.** The Ralston Se HBV framework is mechanistically supported but not yet quantitatively integrated into regulatory thresholds. Whether the Se:Hg molar ratio can be operationalized into a validated quantitative adjustment of MeHg risk, rather than remaining an explanatory factor for differential cohort sensitivity, is an open question.
- **Microbiome-mediated MeHg modulation.** Coe et al. 2023 documents gnotobiotic-mouse evidence that gut microbiota influence MeHg demethylation; human translation is incomplete.

- **PUFA-MeHg risk-benefit quantification.** Net risk-benefit modeling is methodologically complex and current frameworks (FDA-EPA Best/Good/Avoid tiers, EFSA recommendations) treat species-level guidance as the operational summary.

17 | Frequently asked questions

What is methylmercury and how do I get exposed to it from food?

Methylmercury (MeHg) is the organometallic form of mercury that biomagnifies up aquatic food chains and dominates dietary mercury exposure in people who eat fish. For non-occupational populations, exposure is dominated by fish consumption, with large long-lived predatory fish such as shark, swordfish, king mackerel, tilefish, and bigeye tuna carrying the highest loads because they accumulate the metal over their lifespan. Marine mammals like whales and seals, eaten in some subsistence and indigenous diets, are among the highest-MeHg foods documented Ufelle & Barchowsky 2021.

Why is methylmercury considered especially risky during pregnancy?

Methylmercury crosses both the placenta and the blood-brain barrier, and fetal exposure during gestation produces developmental neurotoxicity at levels well below those causing overt symptoms in adults, making the fetus, breastfed infant, and young child the principal at-risk populations. The FDA/EPA fish-consumption advisory specifically targets pregnant women and women of childbearing age because in-utero exposure is the most consequential exposure window FDA 2017. The dose-response anchoring most advisories comes from the long-running Faroe Islands and Seychelles birth-cohort studies.

Which fish are highest and lowest in methylmercury?

MeHg concentration follows trophic level: large, long-lived predatory fish (shark, swordfish, king mackerel, Gulf of Mexico tilefish, bigeye tuna) carry the highest loads because they bioaccumulate the metal over their lifespan. Smaller short-lived fin-fish such as sardines, anchovies, herring, salmon, trout, and tilapia carry substantially less, and shellfish carry less than similarly sized fin-fish due to lower trophic position and shorter lifespan. Because of this, choosing lower-trophic species is the dominant lever for reducing dietary MeHg exposure Li et al. 2024.

What regulatory limits and intake guidelines apply to methylmercury?

Binding maximum levels include the EU Reg. 2023/915 species-specific mercury limits for fishery products (applied as total mercury on the assumption that most mercury in fish is methylmercury) and Codex methylmercury maximum levels for fish, while the FDA sets a nonbinding action level of 1.0 ppm methylmercury in fish EU Reg. 2023/915. For tolerable intake, EFSA set a Provisional Tolerable Weekly Intake of 1.3 µg/kg bw/week EFSA 2012 and JECFA set 1.6 µg/kg bw/week JECFA 2004, while EPA's IRIS reference dose of 0.1 µg/kg bw/day (about 0.7 µg/kg bw/week) is the most conservative EPA IRIS 2001.

Can I be exposed to methylmercury from foods other than fish, like rice?

Yes. Rice is the second-most-important dietary methylmercury source after fish, particularly in Asian populations with low fish but high paddy-rice consumption. Rice grown in contaminated soils (for example artisanal-gold--mining-impacted or chlor-alkali-contaminated watersheds) can carry MeHg in the 5 to 50 µg/kg range, with extreme cases exceeding 100 µg/kg Brombach et al. 2016. One rural-China cohort found that rice-derived

maternal MeHg exposure was associated with child neurodevelopmental endpoints independent of the fish pathway Rothenberg et al. 2021.

How is methylmercury exposure measured or tested for?

Hair mercury is the main long-term biomarker: it reflects systemic exposure over the 2 to 3 months before sampling and runs about 250 times the simultaneous whole-blood level because methylmercury binds preferentially to cysteine residues in keratin. Whole-blood mercury reflects recent (days-to-weeks) exposure and is used clinically and in pregnancy monitoring, while urine mercury mainly reflects inorganic mercury, not MeHg Martinez-Morata et al. 2023. In food, speciation methods such as GC-ICP-MS or LC-ICP-MS directly quantify MeHg, while total-mercury methods like CV-AFS or TDA-AAS are used where the MeHg-to-total-Hg ratio is well characterized.

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Genevieve L. Coe, Ian N. Krout, Mason Munro-Ehrlich, Catherine R. Beamish, Daria Vorojeikina, Daniel R. Colman, et al. · Archives of Toxicology, Vol. 97, pp. 2399-2418 · 2023 · doi.org/10.1007/s00204-023-03548-7
REVIEW
- [25] Advice About Eating Fish — For Those Who Might Become or Are Pregnant or Breastfeeding and Children Ages 1 to 11 Years
U.S. Food and Drug Administration and U.S. Environmental Protection Agency · U.S. FDA and U.S. EPA · 2017 · www.fda.gov
GOVERNMENT
-

STATUS AND LICENCE

Editorially reviewed in-house; no external peer review has been completed on this reference. Published as a preprint with its review state tracked on the article page. Released under CC BY 4.0.

DATA AVAILABILITY

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