Selenium in Seafood Materials

Sakura Yoshida, Mamoru Haratake,* Takeshi Fuchigami, and Morio Nakayama

Graduate School of Biomedical Sciences, Nagasaki University, 1–14 Bunkyo-machi, Nagasaki, 852–8521 Japan

(Received February 1, 2011)

Research interests in studying the biochemical nature of selenium have increased and the importance of this element as an essential micronutrient in many organisms has been well recognized. Selenium occurs in proteins in the form of the 21st amino acid, selenocysteine (SeCys or Sec). In this review, we describe the speciation analysis of the fish-specific selenoproteins and non-proteinous selenium compounds, and the nutritional bioavailability of selenium from seafood materials. Selenium is essential to fish and shellfish. The selenoproteomes (sets of SeCys-containing proteins) of fish are greater in number than those of mammals (25 selenoproteins in humans); at 30–37 selenoproteins, the selenoproteomes of fish are among the largest known. The same core selenoprotein families are found in mammals and fish. In addition, fish have several species-specific selenoproteins [fish 15 kDa selenoprotein-like protein (Fep15), selenoprotein J and selenoprotein L] that are missing in mammals. Actually, not only proteinous selenium species like selenomethionine (SeMet) and SeCys derivatives, but also many non-proteinous organic ones were detected in fish and shellfish samples. Although the selenium contents in seafood are higher than in terrestrial foodstuffs, little is known about the chemical forms of organoselenium species in seafood. The nutritional bioavailability of selenium from seafood appears to be dependent on the fish and shellfish species and/or place where they are produced; some seafood gives rise to a high bioavailability of selenium, which is comparable to that of wheat and beef. Fish and shellfish materials are major dietary sources of selenium for the Japanese population (∼60% of daily intake). Seafood materials appear to contain nutritionally effective organoselenium compounds that have not yet been chemically identified.

Key words —— Fish, shellfish, seafood, selenium, selenoprotein

INTRODUCTION

Selenium was discovered by the Swedish chemist Berzelius in 1817.1,2) Since the first report of its biological importance by Schwartz and Foltz in 1957,2) research interests in studying the biochemical nature of this trace element have increased and the importance of selenium as an essential micronutrient in many organisms has been well recognized. Selenium occurs in proteins in the form of the 21st amino acid, selenocysteine (SeCys or Sec); eukaryotes have variable sets of SeCys-containing proteins (selenoproteomes), which are from zero selenoproteins in the higher plants and fungi to more than 30 in fish and algae.3) Because selenium is one of the micronutrients whose deficiency and toxic levels are close to each other, it is important to know its abundance and deficiency in foodstuffs and to estimate its appropriate balance. A reference nutrient intake (RNI) in the U.K., and the recommended dietary allowance (RDA) in the U.S.A. and Japan are currently set at 75, 55 and 30 µg-selenium day−1 for an adult male, respectively.

Nutritional selenium is thought to come from a variety of selenium compounds in dietary sources, mostly in organic forms such as selenomethionine (SeMet), SeCys and their derivatives. While inorganic selenite (SeO32−) is rare as a chemical form of the dietary source compounds, it is the most frequently used effective one for selenium supplementation of medical treatments. Plant food sources of selenium contain mostly SeMet, but selenium-enriched yeast (a common selenium supplement form) is also found to contain significant amounts of selenite.4,5)

The selenium content of food and beverages geographically varies both within and between coun-
tries and/or areas. The selenium contents of animal foodstuffs basically reflect the selenium content of their consumed diet,6 whereas the selenium content of plants is directly affected by the selenium concentrations in the soil in which they are grown. Fish can take up selenium from the water and/or by eating other marine species in the food chain or web. The accumulation of selenium in marine animals from dietary sources (phyto- and zooplanktons) is more important than that directly obtained from seawater.7

Selenium biology in humans, other animals and plants have been well covered in many books and reviews.8,9 Selenium species in food products from terrestrial plants and animals are also reviewed in a recent publication.10 In this review, we focus on the speciation analysis of fish-specific selenoproteins and non-proteinous selenium compounds, and the nutritional bioavailability of selenium from seafood to be consumed.

SELENOPROTEINS IN FISH AND SHELLFISH

Currently, 25 selenoproteins are identified in humans based on a selenoproteome analysis (cf. 24 selenoproteins in mouse and rat),11 and their physiological roles and functions are being investigated.9,12–14 Selenoproteins are ubiquitously expressed in all organs and tissues, such as glutathione peroxidases (GPxs), thioredoxin reductases and iodothyronine deiodinases. The best-known selenoproteins are part of the GPx family (GPx-1, GPx-2, GPx-3, GPx-4 and GPx-6) that can catalyze the reduction of certain peroxide species (R-OOH) to the corresponding alcohols (R-OH) at their active center SeCys residue.9 More specifically, phospholipid hydroperoxide GPx (GPx-4) is the only antioxidative enzyme that can directly reduce phospholipid hydroperoxides generated in biological membranes, which plays a critical role in the developmental process and biological activity.15,16 It has been shown that selenoproteins can be a thousand times more effective in catalysis than their cysteine (Cys) homologs.17 Such a greater effectiveness of SeCys in catalysis is likely one of the major reasons that nature has developed selenium-dependent metabolic pathways and the specific machinery used for selenium insertion into proteins.

Selenoproteins are basically present in bacteria, archaea and eukaryota. However, some organisms do not use SeCys. For example, as yeast and higher plants lost the SeCys insertion machinery during evolution, they do not synthesize selenoproteins, and instead utilize Cys homologs of some selenoproteins.3,18 Selenium is essential to fish and shellfish,19 and they can synthesize selenoproteins using the SeCys insertion machinery.20–22 Several selenoproteins in fish, including GPx, have been identified and characterized. Fish GPx is purified in the liver of the Southern bluefin tuna (Thunnus maccoyii), which is present in a homotetramer with a native molecular mass of 85 kDa and a subunit molecular mass of approximately 24 kDa.23 The Southern bluefin tuna GPx is structurally similar to the classical GPx-1 found in the liver and red blood cells, the gastrointestinal GPx-2 and the plasma GPx-3 of mammals.

Marine animals have more selenoproteins than terrestrial animals. The selenoproteomes of fish are greater in number than those of mammals; at 30–37 selenoproteins, the selenoproteomes of fish are among the largest known.3 The same core selenoprotein families are found in mammals and fish. In addition, fish have several species-specific selenoproteins [fish 15 kDa selenoprotein-like protein (Fep15), selenoprotein J (SelJ) and selenoprotein L (SelL)] that are missing in mammals, as well as several SeCys-containing copies of selenoproteins T, U and W (SelT1a, b and SelT2, SelU1, 2 and 3, SelW1, 2a and 2b), and two forms of the selenoprotein P (SelPa and SelPb).3

Fep15, absent in mammals, can be exclusively detected in fish and only in the SeCys-containing protein.24 Fep15 is distantly related to members of the 15 kDa selenoprotein (Sep15) family. SeCys in Sep15 is present in the Cys-glycine (Gly)-SeCys motif that is a putative redox site, whereas Fep15 does not have Cys in the vicinity of SeCys. Moreover, the Fep15 sequences have no conserved Cys at all, and several Fep15s do not have any Cys. If SeCys has as an antioxidative activity like the GPxs, it is likely converted into selenenic acid (–SeOH) or selenenylsulfide (–Se–S–) is formed with a thiol of Cys in another protein or with a low-molecular-mass thiol such as glutathione. The biological function of this protein is still unclear.

SelJ was first discovered in the genome of the teleost fish Tetraodon nigroviridis.25 Later, its preferential and homogeneous expression was found in the eye lens during the early stages of the zebrafish (Danio rerio) development.26 This selenoprotein has a restricted phylogenetic distribution and, in
contrast to all known eukaryotic selenoproteins, is not involved in mammalian genomes, not even as a Cys homolog. In addition, SelJ is assumed to play a structural role, although most selenoproteins have enzymatic functions.

SelL was identified in diverse aquatic organisms, including fish, invertebrates, and marine bacteria. This selenoprotein contains two SeCys residues separated by two other residues to form a SeCys-X-X-SeCys motif (two SeCys separated by two X residues) similar to the catalytic Cys-X-X-Cys motif (two Cys separated by two X residues) in thioredoxin, which suggests a redox function of this selenoprotein.

Organisms living in aquatic habitats, such as fish, amphibians and some marine invertebrates, possess a particularly greater number of SeCys residues. For example, the number of SeCys residues in SelPa is higher; 16–17 in fish, as opposed to 7–15 in mammals. Particularly, SelP of the sea urchin involves 28 SeCys residues.

Several selenoproteins in fish have homologs in mammals in which Cys is present in place of SeCys (SelU (SelU1, SelU2 and SelU3), a SelW-like protein radixin (Rdx) 12 and GPx-6). In contrast, no fish could be found that had Cys orthologs of mammalian selenoproteins. Lower SeCys contents of SelP and unidirectional SeCys to Cys transitions in vertebrate selenoproteins suggest a trend toward the reduced utilization of selenium in mammals. Larger selenoproteomes in aquatic organisms may result from several marine-specific factors influencing the SeCys utilization, such as availability of selenium, gradients of temperature, pH, pressure, oxygen content, chemical environment, etc.

The physiological functions of human selenoproteins have not yet been completely revealed. A study of selenoproteins using fish, e.g., the zebrafish, could provide useful information, because the selenoproteome of fish contains all the mammalian selenoproteins.

**NON-PROTEINOUS SELENIUM SPECIES**

A speciation analysis of selenium in various foodstuffs has been performed for past several decades (Fig. 1). For example, SeMet, glutathione selenotrisulfide, selenite and selenate were detected in selenized yeast. Selenium-enriched plant foods (e.g., onion, garlic, shi-itake mushroom) and selenium-accumulating plants (e.g., Indian mustard) contain the selenoamino acids and their derivatives. To date, the speciation analyses of biological samples have been mostly carried out using selenium-enriched plants. Several selenium compounds were identified from certain plant foods, while the selenium species in seafood are hardly known probably due to the extremely low selenium contents as compared with such selenium-enriched plant food.

Selenium is known to interact with several metal elements such as mercury. Ganther et al. showed that tuna contained enough selenium to modify the methylmercury toxicity, that tuna diets reduced the methylmercury toxicity in Japanese quail more than did diets based on plant sources of protein, and that tuna having a high content of mercury tended to accumulate selenium with mercury in a 1 : 1 molar ratio. Selenium was established as a naturally occurring antagonist in marine fish at levels capable of modifying the methylmercury toxicity. Selenium has a protective effect regarding the toxicity of methylmercury and form an equimolar complex. Cabanero et al. investigated the bioaccessibility of selenium and mercury in fish samples [tuna (Thunnus spp.), swordfish (Aphanopus carbo), sardine (Sardina pilchardus)] by an in vitro gastrointestinal digestion method. The selenium and mercury bioaccessibility was found to be dependent on the type of fish analyzed. Simulated human gastric and intestinal digestion led to a high selenium bioaccessibility and low mercury bioaccessibility, and no modification during digestion of both species was found in all the fish samples. They concluded that the potential toxicity of fish cannot be independently evaluated by analyzing the total mercury or methylmercury content, but also the selenium content that could significantly influence the mercury bioaccessible fraction.

George et al. showed that mercury in fish [swordfish (Xiphias gladius)] and fish digested with simulated gastric fluid was coordinated by a single thiolate donor, which resembled Cys. For the selenium, they found a mixture of organic forms that resembled SeMet and an aliphatic selenenylsulfide (–Se–S–). Furthermore, they detected a methylmercury-Cys form in human hair samples taken from individuals with a high fish consumption.

Önning and Bergdahl separated the water-soluble selenium species in commonly-eaten fish by size-exclusion chromatography with on-
line detection by inductively coupled plasma mass spectrometry (ICP-MS).\textsuperscript{45,46} Cod (\textit{Gadus morhua}), salmon (\textit{Salmo salar}), rainbow trout (\textit{Oncorhynchus mykiss}) and eel (\textit{Anguilla anguilla}) mostly had the soluble species (76–88%) in a high-molecular-mass range (>10 kDa). Mackerel (\textit{Scomber scombrus}), herring (\textit{Clupea harengus}) and flat fish contained 0.26–0.50 µg-selenium g\(^{-1}\) in the wet state of which 23–34% was soluble. Half of the selenium species from mackerel and herring was separated in a low-molecular-mass range (<10 kDa), while all the flat fish, such as plaice (\textit{Pleuronectes platessa}), turbot (\textit{Psetta maxima}), flounder (\textit{Platichthys flesus}) and dab (\textit{Limanda limanda}) contained large amounts of low-molecular-mass organoselenium compounds (<2 kDa). SeMet and selenocystine (SeCyst) were not detected in any of the fish tested in their study.

Quijano \textit{et al.} analyzed the selenium species in tuna and mussel by enzymatic digestions and subsequent reverse-phase high-performance liquid chromatography in conjunction with ICP-MS. The total selenium contents were 1.3–4.6 µg-selenium g\(^{-1}\) for tuna and 1.6–1.8 µg-selenium g\(^{-1}\) for mussel. Their analytical method determined the organic [trimethylselenonium ion (TMS), SeCyst, SeMet and selenoethionine] and inorganic selenium species (selenite and selenate), but only TMS and SeMet were found in the samples. Unknown selenium species were also detected in tuna samples. The sum of the identified selenium species in the samples was only about 30% of the total selenium present in the enzymatic extract despite the fact that recoveries of the total hydrolyzed selenium were 93–102%.\textsuperscript{47}

Moreno \textit{et al.} applied the same procedure for the fractionation of selenium species in oyster (\textit{Crassostrea gigas}) by aqueous extraction. The aqueous extract contained 35 ± 3% of the total selenium content (1.22 ± 0.03 µg-selenium g\(^{-1}\)). The selenium species found in oyster tissues were TMS (9.8 ± 0.8%) and SeMet (46 ± 6%).\textsuperscript{48} Moreno \textit{et al.} also reported that SeMet within the range of 0.2–600 µg-selenium g\(^{-1}\) was quantified in selected tissues, but SeCyst was not identified in tuna, trout, krill, oyster and mussel. TMS was quantified (0.1–
0.3 μg-selenium g⁻¹) in oyster, mussel and trout. Inorganic selenium as selenite was found in krill.⁴⁹ In addition, several unidentified organoselenium species were detected.

Wang et al. detected inorganic selenium and selenenate in dogfish (Scyllorhinus canicula) and swordfish (Xiphias gladius) muscle by microwave-assisted extraction (35% selenium recovery) and ion chromatography with on-line detection by ICP-MS. Unknown organoselenium compounds were also detected besides the inorganic selenium.⁵⁰

Siwek et al. extracted approximately 24% of the total selenium of Antarctic krill (Euphausia superba, 2.4 μg-selenium g⁻¹ in dry state). They found that 80% of the extracted selenium was from organoselenium compounds with a molecular mass of 150–600 Da and the rest was bound to proteinous materials. A further analysis of the low-molecular-mass hydrolysates by HPLC-ICP-MS revealed the involvement of SeMet, SeCys and its derivatives. The inorganic selenium species was negligible.⁵¹

Huerta et al. compared four procedures (microwave digestion, methanol/HCl extraction, sodium dodecyl sulfate leaching, and enzymatic hydrolysis) for the extraction of selenium species from a cod muscle sample; enzymatic hydrolysis was the most effective (70% selenium recovery). Reversed-phase and size exclusion HPLC analyses showed that most of the selenium in the sample is associated with proteins, SeMet turns out to be the main organoselenium compound in the enzymatic hydrolysat. As SeMet does not appear after the methanol/HCl extraction, SeMet is not probably free but unspecifically incorporated into proteins in place of methionine.⁵²

Modern mass spectrometric analyses, such as matrix assisted laser desorption ionization time of flight mass spectrometry (MALDI TOF-MS) and electrospray ionization mass spectrometry (ESI-MS) are powerful techniques for the determination of the chemical structure of unknown selenium species according to its characteristic stable isotope pattern.³¹–³⁴ X-ray absorption near edge structure (XANES) spectroscopy is also useful for the detection of selenium species. This analytical technique is non-destructive and able to distinguish the chemical form of selenium.⁴³,⁴⁴,⁵³,⁵⁴ Misra et al. investigated the unique metabolism of selenite, selenite and SeMet in the isolated hepatocytes of rainbow trout (Oncorhynchus mykiss) by XANES spectroscopy besides other biochemical analyses; the inorganic selenium compounds were metabolized into elemental selenium, while a major metabolite of SeMet was SeCyst.⁵⁴

Currently, SeCys is thought to be a major selenium species in animal foodstuffs, since most of them involve SeCys that is incorporated into the selenoproteins, but organoselenium species other than selenoamino acids in fish are hardly ever observed. Although the selenium contents of seafood are higher than in terrestrial foodstuffs, little is known about the chemical forms of the selenium species in seafood. Actually, not only proteinous selenium species like SeMet and SeCys derivatives, but also many low-molecular-mass non-proteinous ones were detected in fish and shellfish samples. Many flat fish such as plaice contain low-molecular-mass selenium species other than SeMet and SeCys, but their chemical structures have not yet been identified. In most of the speciation studies, only using the limited standard materials could identify several selenium species, whereas unidentified peaks of which their retention times were not consistent with those of the standard materials still need to be evaluated.

Recently, Yamashita and Yamashita separated an organoselenium compound, selenoneine (2-selenyl-Nα,Nα,Nα-trimethyl-L-histidine) from the blood of bluefin tuna (Thunnus orientalis).⁵⁵ The chemical structure of this compound was determined by ESI-MS and ¹H- and ¹³C-nuclear magnetic resonance (NMR) techniques (Fig. 1). It is a selenium-analog of ergothioneine that was found in ergot and human blood. Selenoneine appears to show a radical-scavenging activity, although the biological function of selenoneine is not yet known. Anan et al. also detected selenoneine besides selenosugar and TMS in the liver of sea turtles (Eretmocheles imbricata and Chelonia mydas).⁵⁶ It should be noted that the selenium concentrations of both biological samples (several-ten micromolar) were originally much higher than the other fish samples described above (sub-micromolar or less).

**BIOAVAILABILITY OF SELENIUM FROM SEAFOOD**

In general, food and beverages are the source of selenium for the general population and the selenium bioavailability is thought to mainly come from organoselenium compounds (generally more than 80%). Food with a higher selenium content is not necessarily a better selenium source, but the
bioavailability of selenium in food must also be considered. The nutritional bioavailability (or amount absorbed and used by the organism) of selenium from dietary sources is dependent on their selenium content and the chemical form of the selenium species to be taken.57,58)

Although the selenium content in fish is high, there are fewer reports on the bioavailability of selenium from seafood than from wheat, cereal, eggs, meats, etc.59–62) In some cases, fish is not a rich source of bioavailable selenium, due in part to its high mercury content and other heavy metals, which bind to selenium.10) Due to the formation of an insoluble complex with heavy metals, such as mercury, selenium from seafood, e.g., tuna, was thought to be less bioavailable than that from beef and wheat. Alexander et al. compared the bioavailability of selenium in several tuna products with that in wheat products with the rats GPx activity in the liver, kidney and whole blood as an indicator of the bioavailability (selenium contents in diets: 0.05, 0.10 and 0.15 µg-selenium g⁻¹-diet). A significantly lower GPx activity was found in the tuna products as compared to the wheat ones. Food processing does not appear to affect the bioavailability, but selenium appears to be more available in wheat products than in tuna.63)

On the other hand, recent papers showed that the bioavailability of selenium from fish was higher than that of selenite and SeMet. Mutanen et al. investigated the bioavailability of selenium in four seafoods, i.e., crab (Callinectes sapidus), oyster (Crassostrea virginica), shrimp (Penaeus duorarum) and Baltic herring (Clupea harengus), which are known to contain high levels of selenium.64) Weanling male rats were fed a selenium-deficient Torula yeast diet for 4 weeks followed by either continued depletion or repletion for 4 weeks with a 0.05–0.2 µg-selenium g⁻¹-diet. Except for the oyster, the absorption of selenium in all these seafoods was close to that of selenite as the plasma GPx activity was used as a criterion. Only herring selenium had a bioavailability for hepatic GPx activity restoration comparable to that of selenite. The bioavailability increased with increases in the amount of selenium from crab, oyster and shrimp in their diets. They considered several factors affecting the bioavailability, such as protein, methionine and mercury contents in the diets.

Wen et al. assessed the bioavailability of selenium from flounder and tuna in comparison to various meats.65) Female weanling rats were fed a selenium-deficient diet for 6 weeks and selenium-adequate diets containing 0.05 µg-selenium g⁻¹ as various foodstuffs for the next 9 weeks. Selenium from the flounder and tuna was the most efficient in restoring the hepatic GPx-1 activity to the same level as the control diet; the relative enzyme activity from the different dietary groups compared with control rats (100%) was: flounder 106%, tuna 101%, pork 86%, selenite 81% and SeMet 80%. Selenium from the flounder and tuna was also effective to restore the selenium in the liver and muscle.

Ørmsrud and Lorentzen showed a high bioavailability of selenium from the SeMet-enriched fillets of Atlantic salmon (Salmo salar).66) Torula yeast-based diets supplemented with 0.05–0.2 µg-selenium g⁻¹-diet in the form of sodium selenite or selenium from raw or cured salmon were fed to selenium-deficient male weanling rats for 30 days, and the selenium content in the tissues and the plasma GPx activity were assessed. The fractional apparent selenium absorption and fractional retention was in the order of raw salmon > cured salmon > selenite. The higher bioavailability of the raw and cured salmon than the selenite was supported by selenium accumulation in the tissues and induction of the GPx activity. The bioavailability of selenium from these fish also appeared to be dependent on their processing. On the contrary, Dumont et al. reported a low bioavailability for selenium species in Atlantic salmon: SeMet > selenite > SeCyst > fish meal.7)

Yoshida et al. studied the selenium bioavailability of the dark muscle from tuna. Male weanling mice were fed on a Torula yeast-based selenium-deficient diet for 3 weeks, and then the basal diet, a diet supplemented with a 0.05 or 0.25 µg-selenium g⁻¹ in the dry state as defatted dark muscle of the tuna or sodium selenite for another week. The tuna-supplemented diet resulted in a lower concentration of selenium in the liver of mice than the selenite-supplemented diet, whereas the mice fed 0.25 µg-selenium g⁻¹ as tuna showed a higher hepatic GPx activity.67)

Fox et al. indicated that selenium in fish is a highly bioavailable source of dietary selenium, and that cooking the fish did not affect the selenium absorption and retention.68) Trout fed ⁷⁸Se-labelled selenized yeast, ⁷⁷Se-labeled selenized yeast and ⁸²Se-labelled sodium selenate in water were used to clarify the contribution of fish to the overall dietary intake of selenium. Healthy male volunteers consumed cooked or salted selenium-enriched
trout or yeast. Blood, urine and feces were collected to determine the absorption and retention ratio of the selenium. The retention of selenium from cooked and salted fishes was significantly higher than that from yeast and selenate. The results demonstrated that the processing of fish did not influence the apparent absorption and retention of the selenium. Selenium-deficient diseases and related pathologies have never been reported in Japan. Miyazaki et al. reported that seafood materials are the major dietary sources of selenium for the Japanese population (\( \sim 60\% \) of daily intake).\(^{69}\) Niboshi is a commonly used foodstuff that is processed from Japanese anchovy (Engraulis japonicus), and its extract is used as a general base seasoning for a wide variety of Japanese cuisines, just like the fond de veau for the French cuisine. Haratake et al. demonstrated that the Niboshi contains a relatively high concentration of selenium (1 µg-selenium g\(^{-1}\)), and selenium from the Niboshi and its extract can effectively restore the selenium concentration in the liver and activity of hepatic cellular GPx in dietary selenium-deficient mice.\(^{70}\)

**CONCLUSIONS**

Selenoproteins occur in both eukaryotes and prokaryotes, but the selenoproteome is highly variable among organisms, and certain organisms do not utilize SeCys at all. Fish and shellfish apparently retain, and in some cases, increase their selenoproteomes, whereas the selenoproteomes of some terrestrial organisms are reduced or completely lost. Many selenoproteins originate at the base of the eukaryotic domain and suggest that the sea environment that influences the selenium utilization plays a critical role in the fish selenoproteomes. Although recent advances in analytical techniques, especially mass spectrometry, significantly contribute to the speciation of low-molecular-mass organoselenium compounds in foodstuffs, selenium species in dietary seafood materials are still poorly known at present. Fish, shellfish and other marine animals are likely to have chemically diverse low-molecular-mass non-proteinous selenium species other than selenoamino acids and selenoproteins, which may be responsible for their diets and/or fish-specific metabolic pathways. The nutritional bioavailability of selenium from seafood appears to be dependent on the fish and shellfish species and/or place where they are produced; some seafood gives rise to a high bioavailability of selenium, which is comparable to that of wheat and beef. In general, the bioavailability of chemical species is affected by their chemical forms and/or other dietary components. Seafood materials appear to contain nutritionally effective low-molecular-mass organoselenium compounds that have not yet been chemically identified.

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