Chapter 8
Preliminary Estimates of the Export of Omega-3 Highly Unsaturated Fatty Acids (EPA + DHA) from Aquatic to Terrestrial Ecosystems

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8.1 Introduction

In recent decades polyunsaturated fatty acids (PUFA) have come to be recognized as compounds with considerable physiological importance for animals at all taxonomic levels, including humans. Animals do not have the enzymes necessary to insert double bonds in fatty acid molecules in positions closer than the 7th carbon (designated n-7 or ω7) from the methyl end of the molecule; therefore, 18-carbon-long PUFA such as linoleic acid (LIN; 18:2n-6) and α-linolenic acid (ALA; 18:3n-3) are essential dietary nutrients (Fig. 8.1). These two essential PUFA are primarily synthesized by plants (both vascular plants and algae) and by some fungi (Fig. 8.1). These PUFA are the biochemical precursors of the most physiologically active PUFA: arachidonic acid (ARA; 20:4n-6), eicosapentaenoic acid (EPA; 20:5n-3), and docosahexaenoic acid (DHA; 22:6n-3). Higher plants cannot desaturate and elongate ALA to EPA and DHA; however, many algae can perform these reactions (Fig. 8.1, and see Sect. 8.2 for details). Although animals, including humans, can desaturate and elongate the parent ALA to EPA and DHA (Fig. 8.1, Gerster 1998 concludes that this conversion is "unreliable and restricted" in humans; see also Plourde and Cunnane 2007) the efficiency of this process, and the tissue-specific requirements for particular PUFA, are quite variable among animal species and developmental stages within species. Nevertheless, the n-3 highly unsaturated fatty acids (HUFA[1]) are increasingly understood to play a key role

[1]The two long chain highly unsaturated fatty n-3 fatty acids (i.e. EPA and DHA) will be referred to in this chapter as n-3 HUFA or, for brevity, simply as HUFA.

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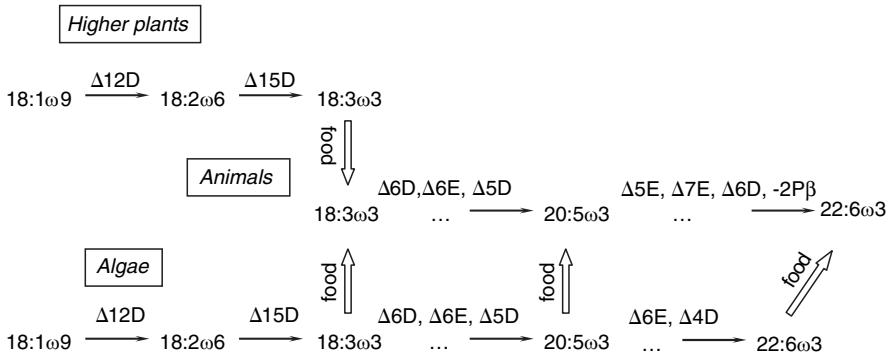

Fig. 8.1 Schematic of n-3 polyunsaturated fatty acids synthesis in different groups of organisms: black arrows – biosynthesis; open arrows – food intake; Δn – number of carbon from carbonyl end of the molecule; *D* desaturase; *E* elongase; $2P\beta$ peroxisomal system of enzymes for β oxidation. Note: for simplicity only one pathway of biosynthesis of 20:5ω3 and 22:6ω3 in algae is depicted, and a number of intermediate fatty acids are substituted by "…"

in the health of all organisms. They have a generally positive impact on animal (and human; see Chap. 14) health due to their effects in preventing/mitigating cardiovascular diseases, ontogenesis (particularly neural development), "dysfunctional" behaviors (e.g., aggression, homicide), atherosclerosis, neural disorders, and, potentially, some cancers, as well as autoimmune diseases (e.g., Arts et al. 2001; Lauritzen et al. 2001; Broadhurst et al. 2002; Copeman et al. 2002; Silvers and Scott 2002; Aktas and Halperin 2004; Hibbeln et al. 2004, 2006; Simopoulos 2004a). In addition, DHA is known to play a pivotal role in the health and function of the vertebrate retina and nervous tissues (SanGiovanni and Chew 2005).

In this chapter we consider evidence that algal-derived HUFA are an important, or, even the main source of dietary-derived HUFA for many terrestrial animals (Fig. 8.1). We also explore the alternative hypothesis that, in terrestrial food webs, HUFA in sufficient abundance may be commonly found, therefore lessening the importance of aquatic-derived HUFA. A second hypothesis, and one that we cannot fully resolve due mainly to a paucity of existing data, is that terrestrial animals can simply desaturate and elongate dietary ALA (Fig. 8.1) to meet whatever requirements they may have for HUFA.

8.2 HUFA in Aquatic and Terrestrial Ecosystems

Among organisms in the biosphere, algae, and, in particular, diatoms, cryptophytes, euglenoids, and dinoflagellates, can de novo synthesize high amounts of HUFA (Fig. 8.1). Once synthesized at the level of primary producers, HUFA are transferred and can accumulate, at progressively higher trophic levels, in the biomass of aquatic organisms. Therefore, aquatic ecosystems occupy the unique position on earth as the principal dietary source of n-3 HUFA for all animals, including inhabitants of terrestrial ecosystems. There are three critical assumptions that logically follow

the previous statement, i.e., that terrestrial animals: (a) cannot obtain sufficient HUFA solely from terrestrially based foods, (b) cannot synthesize n-3 HUFA (from ALA) at levels sufficient to meet their needs, and (c) require adequate HUFA levels in the diet for optimal physiological performance, i.e., HUFA are beneficial. Several lines of evidence can be advanced to support to these three assumptions.

First, it is necessary to point out that the majority of unsaturated fatty acids in higher plants are the C_{18} compounds: oleic, linoleic, and α-linolenic acids (Shorland 1963; Harwood 1996). Higher plants generally cannot convert 18-carbon chain (C_{18}) PUFA to HUFA (Heinz 1993; Tocher et al. 1998, Fig. 8.1). In contrast, the lower plants, i.e., some groups of the eukaryotic microalgae, and a few fungi (e.g., *Saprolegnia sp.* and *Mortierella alpina*) possess the enzymatic systems for de novo biosynthesis of HUFA and can produce significant amounts of these FA (Cohen et al. 1995; Tocher et al. 1998; and, for fungi see Leonard et al. 2004, Fig. 8.1). Thus, even for some of the most oil-rich tissues of terrestrial plants (i.e., the seed crops and their wild relatives), genetic intervention is needed in order to achieve a substantial HUFA content (Robert 2006; Damude and Kinney 2007). Another example is that the seeds of common tree species (pine, spruce, larch), which are commonly consumed by terrestrial herbivores, also do not contain HUFA in any appreciable quantities (Wolff et al. 2001). Wild edible leafy plants can also be shown to contain only C_{18} PUFA (Simopoulos 2004b). Finally, studies on terrestrial vegetative matter entering streams and lakes have demonstrated that this material does not contain HUFA (Mills et al. 2001).

Second, many invertebrate species consume primary producers directly and may themselves be consumed by predators at higher trophic levels. Recognizing that there is some conservatism with respect to incorporation of dietary FA into invertebrate tissue (see Chap. 6), a comparison of FA profiles of aquatic versus terrestrial invertebrates should shed light on: (a) the relative differences in HUFA contents of aquatic versus terrestrially derived dietary plant materials, (b) their subsequent retention in primary consumers, and (c) the potential for their transfer to consumers at higher trophic levels. Although there are some exceptions (e.g., Nor Aliza et al. 2001), the majority of terrestrial insects examined so far have very low HUFA concentrations (Uscian and Stanley-Samuelson 1994; Howard and Stanley-Samuelson 1996) relative to aquatic insects, which have been shown to be generally rich in HUFA (Hanson et al. 1985). Thus, terrestrial insects, as one of the key food sources for terrestrial predators, may be, in general, unlikely candidates to supply the majority of the HUFA to terrestrial predators at higher trophic levels.

Third, terrestrial predators show reductions in the n-3 PUFA and HUFA concentrations as the quantity of aquatic food in their diets declines. Three examples include: (a) small carnivorous mammals show a significant decline in their DHA to linoleic acid (18:2n-6) ratios as their dependence on aquatic food webs decreases (Koussoroplis et al. 2008), (b) long-term decreases in the concentrations of C_{18} and C_{20} n-3 PUFA have been observed in herring gulls in the Great Lakes as their forage base shifted from primarily aquatic to terrestrial diet items (Hebert et al. 2008), and (c) carnivorous reptiles consuming seabirds on small islands have higher plasma EPA and DHA contents than conspecifics on nearby islands where rats (terrestrial prey)

form a higher percentage of the diet (Blair et al. 2000). Taken together such observations suggest that n-3 HUFA concentrations in terrestrial predators will generally increase as their consumption of aquatic prey increases.

Finally, we must ask – do terrestrial animals actually need dietary HUFA? This is a question with far-reaching implications, and we provide several lines of reasoning to suggest that this may often be the case. It is clear that the ability to elongate and desaturate ALA to EPA and DHA, at levels that are sufficient to supply them with optimum concentrations of HUFA, is not equally prevalent and/or efficient among animal species and/or among tissues (Mitchell et al. 2007; Leonard et al. 2004) and also that HUFA requirements might differ seasonally (Pruitt and Lu 2008). African camilids and rodents, for example, have EPA and DHA concentrations that range from very low to nondetectable in their meat (Hoffman 2008), whereas domestic farm animals (cattle, sheep, and especially pigs) contain appreciable levels of both EPA and DHA in their muscle and adipose tissues (Wood et al. 2008). To add to the complexity it is also clear that diet affects the ultimate expression of HUFA concentrations in the meat of vertebrates (Wood et al. 2008) and that the specific requirement for HUFA may be more critical for some developmental stages and/or tissues than others. Further, energy is required to elongate and desaturate C_{18} PUFA to form HUFA and, therefore, conservatively acquiring these materials "pre-formed" in the diet is, at the very least, energetically advantageous. Also, the inherent biochemical properties of EPA and DHA, that give them their special properties, apply universally, i.e., their functional roles in the physiological competency of cell membranes and in maintaining a healthy immune system (e.g., Stanley-Samuelson et al. 1991) is not limited in their applicability to aquatic animals (e.g., see Chap. 10) but extend to terrestrial animals as well (e.g., Geiser et al. 1992; Stanley 2006).

It is already well established that clear physiological benefits accrue to both aquatic and terrestrial animals when they consume adequate levels of HUFA in their diets. This can be assessed in two ways: by examining the effects of offering animals diets that are either HUFA deficient or HUFA sufficient or by adding HUFA to the diet. Such techniques, combined with field studies, have clearly demonstrated the importance of food quality (i.e., of contents of essential nutrients, including HUFA) for aquatic animals, especially for daphnids (e.g., Müller-Navarra 1995; Gulati and DeMott 1997; Gladyshev et al. 2006a; Danielsdottir et al. 2007). Somatic growth of *Daphnia* correlates with EPA content in seston (i.e., with food quality), rather than with sestonic carbon content (i.e., with food quantity) (e.g., Müller-Navarra 1995; Gladyshev et al. 2006a) even for very low food levels (Boersma and Kreutzer 2002). Most of the evidence for the effects of HUFA content on terrestrial animals comes primarily from laboratory studies of mammals and birds. For example, n-3 HUFA-deficient rats exhibited significantly longer escape latency and poorer memory performance in maze experiments compared with n-3 HUFA sufficient rats (Lim et al. 2005a), and n-3 fatty-acid-deficient mice had impaired learning in a reference-memory version of circular maze, i.e., they spent more time and made more errors in search of an escape tunnel (Fedorova et al. 2007). In birds it has been shown that egg FA composition reflects diet FA composition (Farrell 1998) and birds such as herring gulls were in poorer condition and exhibited

reduced reproductive success in areas where they consumed a higher proportion of terrestrial food (Hebert et al. 2002, 2008). The offspring of domestic cats (carnivores), whose mothers were fed corn-oil based diets, had insufficient levels of EPA and DHA in their brains and retinas (and consequently exhibited delayed photoreceptor responses) which suggested that they had a low biosynthetic capacity to produce these FA (Pawlosky et al. 1997). Rats (omnivores) have also been shown to have a requirement for dietary DHA in order to insure proper brain function (Lim et al. 2005b). Vegetarian, and especially vegan, humans must rely on the internal conversion of ALA to EPA and DHA and, these people have, in addition to lower total lipid levels in their plasma and erythrocytes, plasma EPA and DHA levels that are only 12–15% and 32–35%, respectively, as high as those of nonvegetarians (cited in Davis and Kris-Etherton 2003). Tissue and/or developmental stage-specific needs are also recognized such as the critical requirement for DHA for vision in vertebrates (Politia et al. 2001).

In conclusion, due to the paucity of data and limited number of species examined we can, at present, neither absolutely confirm nor deny a universal dependency for dietary HUFA among terrestrial animals. However, a growing body of evidence suggests that: (a) given the apparent scarcity of these compounds in terrestrial ecosystems, (b) their many recognized physiological benefits, and (c) the probability that they are required by least at some tissues, and/or some developmental stages, and/or during different seasons, this at least remains a real and likely possibility.

Thus, we postulate that the well-established function of waterbodies as a source of drinking water should be augmented by an explicit recognition of their role in supplying terrestrial ecosystems with biochemically and physiologically essential lipids. It is also important to note that aquatic ecosystems differ in their ability to produce HUFA. For instance, water bodies dominated by cyanobacteria have significantly lower relative HUFA production than those dominated by diatoms (Müller-Navarra et al. 2004). Moreover, algae, such as the HUFA-rich diatoms (e.g., Sushchik et al. 2004), are known to accumulate higher levels of HUFA as temperatures decrease – a process referred to as cold adaptation (see also Chaps. 1 and 10). Thus, large-scale processes such as eutrophication and global warming may act either independently, or in concert, to effect an overall decrease in HUFA production in aquatic ecosystems with possible negative implications for surrounding terrestrial ecosystems. At present it is not possible to assess the potential ecological risks associated with decreased HUFA production as a result of anthropogenic impacts and global warming because there are, as yet, no global, or even regional, estimates of the amount of HUFA that is exported from aquatic to terrestrial ecosystems. Thus, we suggest that a concerted effort to quantify HUFA export from aquatic to terrestrial ecosystems, in geographically and climatically diverse regions with different levels of anthropogenic impact, should be attempted. Although we view such an attempt as necessary we also clearly acknowledge that estimates of HUFA export are, by their very nature, and also largely because of the paucity of data, preliminary and incomplete. Thus, this chapter is also intended to stimulate further research on quantifying the role of aquatic ecosystems as *producers* and *providers* of HUFA to terrestrial organisms.

In aquatic ecosystems, HUFA produced by microalgae are transferred to primary consumers such as zooplankton and zoobenthos. Naturally, zooplankton and zoobenthos comprise several trophic levels, i.e., carnivorous animals consume HUFA along with their prey and thus HUFA are bioaccumulated within aquatic food webs (Kainz et al. 2004), as well as recycled within plankton and benthic communities. Nevertheless, although these functional food web links are crucial for aquatic ecosystems, we will not refer to internal aquatic food web dynamics here because such processes are not directly related to HUFA export. Aquatic animals including zooplankton, zoobenthos, and fish can be consumed by water birds (e.g., Hebert et al. 2008) and riparian animals (e.g., Koussoroplis et al. 2008), and their HUFA are thus exported to terrestrial ecosystems. Water birds and riparian animals, in turn, may be consumed by other terrestrial predators or by soil organisms after death. Nevertheless, here we will only focus on the potential export of HUFA from aquatic to terrestrial ecosystems. Besides direct consumption of animals in the aquatic environment by terrestrial animals (e.g., Hilderbrand et al. 1999a), HUFA are also exported from aquatic to terrestrial ecosystems through aquatic insect and amphibian emergence (Fig. 8.2).

These considerations may be attributed primarily to inland waters. Export of HUFA from marine waters to terrestrial ecosystems is believed to be primarily due to shore drift of carrion and seaweeds, and anadromous salmon migrating in rivers (Fig. 8.2). Here we omit the input through seabirds, since colonies of these birds represent closed systems, which are usually somewhat separated from other terrestrial communities. Seabirds usually nest on coastal rocks, or live on ice

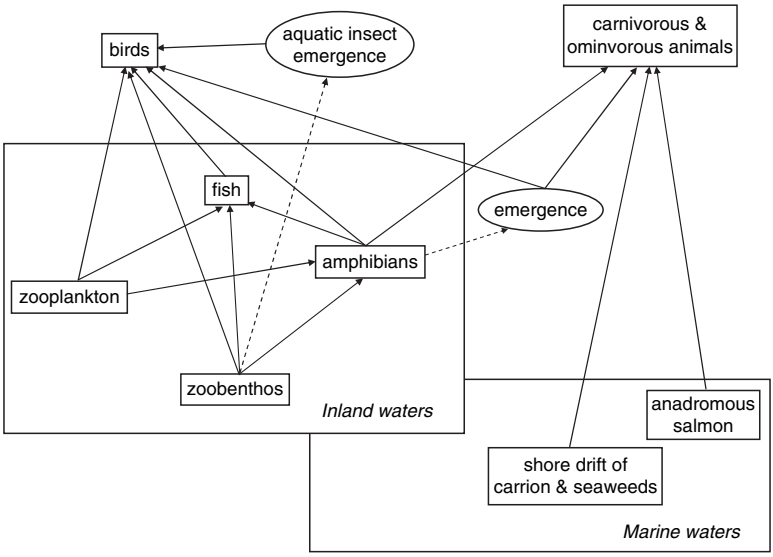

Fig. 8.2 Schematic flow diagram depicting directionality of HUFA fluxes from aquatic to terrestrial ecosystems

shelves (penguins), and therefore exhibit a lower level of connectivity (although, clearly, predation on seabirds by terrestrial animals occurs) with terrestrial systems. Because of this we here consider seabirds as a primarily oceanic rather than a terrestrial fauna.

8.3 Required Measurements

Based on general considerations (Fig. 8.2), we can begin to identify the type of data needed in order to obtain preliminary estimates of the amount of HUFA exported from a particular aquatic ecosystem to adjacent terrestrial ecosystems. Such calculations require knowledge of:

(a) HUFA composition of aquatic animals (e.g., zooplankton, zoobenthos, and fish)
(b) Rations of water birds and riparian animals, fed with aquatic animals
(c) Areal biomass of water birds and riparian animals that feed on aquatic animals
(d) HUFA content of emerging aquatic animals (insects and amphibians)
(e) Emergence intensity
(f) Surface area of the aquatic ecosystems of interest
(g) Surface area of the adjacent terrestrial ecosystems
(h) Metabolic HUFA requirements of carnivorous and omnivorous terrestrial animals and their biomass.

The final point is required in order to gauge whether or not terrestrial organisms might ever be limited by their access to HUFA derived from aquatic ecosystems.

Unfortunately, at present, there are no systematic, quantitative, or even semiquantitative estimates reported for the export of the two essential n-3 HUFA (EPA and DHA; the focus of this chapter) from aquatic to terrestrial ecosystems despite growing evidence that these compounds contribute significantly to maintaining animals in a state of optimal physiological competency (see Chaps. 10, 13, 14). We are aware that our literature survey and resulting estimates will not be comprehensive. There are two main reasons for this. First, there is a general paucity of data in the primary literature in relation to the eight steps outlined earlier, especially for some groups of animals (e.g., amphibians). Second, global estimates, by their very nature, will probably always lack the specificity, completeness, and refinement that more regional estimates may, one day, be able to provide.

Does this mean that the prospect of generating the first ever global estimate of HUFA export from aquatic to terrestrial systems is not worth attempting? We argue against this for two reasons. First, it is important to formally acknowledge, the heretofore unrecognized function that aquatic ecosystems provide as the producers of essential nutrients for the whole biosphere. In order to provide meaning and context to this concept estimates of HUFA flux rates (however preliminary) are required. Second, we seek the indulgence of our readers to allow us this opportunity to develop a conceptual framework from which future estimates may be developed and refined as more data becomes available.

8.4 HUFA Content of Aquatic Organisms

A subset of the available literature data on the HUFA content in aquatic animals and seaweed is summarized in Tables 8.1–8.4. We restrict the freshwater zooplankton data to two locations (Table 8.1; but see Chap. 6 for greater detail). For Cladocera

Table 8.1 Average contents of EPA and DHA, mg g^{-1} of dry weight, in zooplankton organisms of inland waters: *n* = number of samples

Species (taxon)	EPA	DHA	Sum	Ecosystem, Region	*n*	References
Cladocera[a]						
Daphnia spp.	6.3	4.8	11.1	Lakes in north-western Sweden	5	Persson and Vrede (2006)
Bosmina coregoni	7.2	1.3	8.5	Lakes in north-western Sweden	4	Persson and Vrede (2006)
Holopedium gibberum	7.4	0.9	8.3	Lakes in north-western Sweden	15	Persson and Vrede (2006)
Bythotrephes longimanus	8.7	0.8	9.5	Lakes in north-western Sweden	4	Persson and Vrede (2006)
Calanoida[a]						
Arctodiaptomus laticeps	5.6	11.1	16.7	Lakes in north-western Sweden	8	Persson and Vrede (2006)
Heterocope spp.	4.3	8.3	12.6	Lakes in north-western Sweden	8	Persson and Vrede (2006)
Zooplankton >500 μm (*Daphnia*, *Holopedium*, calanoid copepods)	10.8	2.2	13.0	Lakes and reservoirs in British Columbia, Canada	nr	Kainz et al. (2004)
Average for zooplankton			11.4			

[a]Recalculated from the reference data using ratio for zooplankton (Cladocera and Copepoda) 1 g C = 2.75 g dry mass (Alimov 1989)
nr = not reported

Table 8.2 Average contents of EPA and DHA, mg g^{-1} of dry weight, in zoobenthos organisms of inland waters: *n* = number of samples

Species (taxon)	EPA	DHA	Sum	Ecosystem, Region	*n*	References
Insecta						
Chaoborus flavicans	23.6	5.5	29.1	Lake Erken, Sweden	6	Goedkoop et al. (2000)
Trichoptera[a]	10.8	0.8	11.6	Yenisei river, Siberia, Russia	4	Sushchik et al. (2003)
Trichoptera	2.37	0.15	2.5	3 streams in Quebec, Canada	46	A. Mazumder, pers. comm.
Trichoptera, Glossosomatidae	16.1	0.2	16.3	6 streams in Washington State, USA	12	C. Volk, pers. comm.
Ephemeroptera[a]	12.8	tr	12.8	Yenisei river, Siberia, Russia	5	Sushchik et al. (2003)
Ephemeroptera	2.12	0.02	2.1	3 streams in Quebec, Canada	46	A. Mazumder, pers. comm.
Ephemeroptera, Baetidae	13.9	0.3	14.2	6 streams in Washington State, USA	11	C. Volk, pers. comm.

(continued)

Table 8.2 (continued)

Species (taxon)	EPA	DHA	Sum	Ecosystem, Region	*n*	References
Ephemeroptera, Heptagenidae	9.36	0.15	9.5	6 streams in Washington State, USA	15	C. Volk, pers. comm.
Diptera, Simulidae	3.00	0.08	3.1	3 streams in Quebec, Canada	15	A. Mazumder, pers. comm.
Plecoptera, Pteronarcidae	0.72	0.00	0.7	3 streams in Quebec, Canada	15	A. Mazumder, pers. comm.
Chironomidae						
Chironomus spp.	4.0	tr	4.0	Lake Erken, Sweden	18	Goedkoop et al. (2000)
Procladius sp.	6.4	0.6	7.0	Lake Erken, Sweden	6	Goedkoop et al. (2000)
Diamesa baikalensis and unidentified spp.[a]	7.7	tr	7.7	Yenisei river, Siberia, Russia	6	Sushchik et al. (2003)
Oligochaeta[a]	6.3	0.5	6.8	Yenisei river, Siberia, Russia	10	Sushchik et al. (2006)
Amphipoda						
Gammarus lacustris[a]	2.6	1.8	4.4	Wetland ponds, Saskatchewan, Canada	nr	Arts et al. (2001)
Hyalella azteca	3.3	0.4	3.7	Wetland ponds, Saskatchewan, Canada	nr	Arts et al. (2001)
Gammarus fossarum[b]	10.2	2.3	12.5	Struga Dobieszkowska River, Poland	nr	Kolanowski et al. (2007)
Gammarus pulex[b]	3.9	1.2	5.1	Stradanka River, Poland	nr	Kolanowski et al. (2007)
Gammarus roeseli[b]	9.6	3.8	13.4	Notec River, Poland	nr	Kolanowski et al. (2007)
Pontogammarus robustoides[b]	20.9	4.3	25.2	Wloclawski Reservoir, Poland	nr	Kolanowski et al. (2007)
Dikerogammarus haemobaphes[b]	12.6	2.7	15.3	Wloclawski Reservoir, Poland	nr	Kolanowski et al. (2007)
Gammaridae[a]	8.1	1.2	9.3	Yenisei river, Siberia, Russia	6	Sushchik et al. (2003)
Average for zoobenthos			9.8			

tr tracers (<0.1 mg g^{-1} DM); *nr* not reported

[a]Recalculated from the reference using moisture contents Gammaridae 75.3%, Thichoptera 83.8%, Chironomidae 78.0%, Ephemeroptera – 80% and Oilgochaeta – 78%

[b]Recalculated from Figs. 3 and 4 of the reference

averaging the mean values of EPA + DHA of the different species give the following general mean value and standard error (SE) 9.4 ± 0.6 mg g^{-1} of dry weight (DW). For the zooplankton species and groups listed in Table 8.1 the general EPA + DHA average is 11.4 ± 1.1 mg g^{-1} DW. It is clear that increasing the number of studied zooplankton species and water bodies will expand increase our understanding variation of HUFA contents. Nevertheless, at present there is no reason to consider

Table 8.3 Average contents of EPA and DHA, mg g^{-1} of dry weight, in fish of inland waters: n = number of samples

Species	EPA	DHA	Sum	Ecosystem, region	n	References
Abramis brama L. (bream)	2.02	3.25	5.27	Lakes in Sweden	4	Ahlgren et al. (1994)
Alosa pseudoharengus (alewife)	13.7	11.9	25.6	Hamilton Harbour, Ontario, Canada	5	M.T. Arts and M. Koops (pers. comm.)
Ameiurus nebulosus (brown bullhead)	2.39	3.91	6.3	Hamilton Harbour, Ontario, Canada	21	M.T. Arts and M. Koops (pers. comm.)
Anguilla anguilla L. (eel)	4.98	6.86	11.84	Lakes and brackish Baltic, Sweden	8	Ahlgren et al. (1994)
Astyanax fasciatus Cuvier and *Melaniris sardina* Meek	1.2	5.0	6.2	Lakes Xolotlan and Cocibolca, Nicaragua	11	Ahlgren et al. (2002)
Barbus sp. (barbs)	2.17	4.48	6.65	Lakes in Ethiopia	7	Zenebe et al. (1998)
Blicca bjoerkna L. (white bream)	1.88	4.10	5.98	Lakes in Sweden	2	Ahlgren et al. (1994)
Carassius carassius L. (crucian carp)	1.05	3.03	4.08	Lakes in Sweden	2	Ahlgren et al. (1994)
Clarias gariepinus Burchell (catfish)	1.43	4.45	5.88	Lakes in Ethiopia	13	Zenebe et al. (1998)
Cyprinus carpio (common carp)	2.29	4.49	6.78	Hamilton Harbour, Ontario, Canada	9	M.T. Arts and M. Koops (pers. comm.)
Esox lucius L. (pike)	1.31	5.21	6.52	Lakes and brackish Baltic, Sweden	7	Ahlgren et al. (1994)
Gymnocephalus cernuus L. (ruffe)	2.11	4.04	6.15	Lakes in Sweden	5	Ahlgren et al. (1994)
Lates niloticus L. (Nile perch)	0.64	3.62	4.26	Lakes in Ethiopia	3	Zenebe et al. (1998)
Lepomis gibbosus (pumpkinseed)	1.90	6.04	7.94	Hamilton Harbour, Ontario, Canada	4	M.T. Arts and M. Koops (pers. comm.)
Leuciscus idus L. (ide)	2.28	4.94	7.22	Lakes in Sweden	1	Ahlgren et al. (1994)
Lota lota L. (burbot)	2.58	4.57	7.15	Lakes in Sweden	4	Ahlgren et al. (1994)
Lucioperca lucioperca L. (pike-perch)	1.07	4.18	5.25	Lakes in Sweden	2	Ahlgren et al. (1994)
Micropterus salmoides (large mouth bass)	1.62	4.61	6.23	Hamilton Harbour, Ontario, Canada	9	M.T. Arts and M. Koops (pers. comm.)
Notropis atherinoides (emerald shiner)	4.59	5.70	10.29	Hamilton Harbour, Ontario, Canada		M.T. Arts and M. Koops (pers. comm.)
Oncorhynchus mykiss W. (rainbow trout)	3.38	10.18	13.56	Lakes and reservoirs in British Columbia, Canada	12	Kainz et al. (2004)
Oreochromis niloticus L. (tilapia)	0.86	4.80	5.66	Lakes in Ethiopia	18	Zenebe et al. (1998)
Perca fluviatilis L. (perch)	1.27	4.49	5.76	Lakes in Sweden	9	Ahlgren et al. (1994)

Rutilus rutilus L. (roach)	2.54	5.00	7.54	Lakes in Sweden	9	Ahlgren et al. (1994)
Tinca tinca L. (tench)	1.62	2.67	4.29	Lakes in Sweden	1	Ahlgren et al. (1994)
Thymallus arcticus Pallas (Siberian grayling)	3.61	8.68	12.29	Yenisei river, Siberia, Russia	44	Sushchik et al. (2007)
Thymallus thymallus L. (European grayling)	4.65	9.37	14.02	Rivers in Sweden	8	Ahlgren et al. (1994)
Thymallus thymallus L. (European grayling)	3.56	6.97	10.53	River Vindelalven, Sweden	18	Ahlgren et al. (1999)
Average for fish			8.1			

Table 8.4 Average contents of EPA and DHA, mg · g^{-1} of dry weight, in marine organisms: *n* = number of samples.

Species (taxon)	EPA	DHA	Sum	Ecosystem, Region	*n*	References
Macroalgae						
11 species of seaweeds	1.3	<0.01	1.3	French Brittany coast	nr	Fleurence et al. (1994)
Invertebrates						
Copepods[a]	13.8	10.9	24.7	Norwegian Sea	14	Ahlgren et al. (2005)
Copepods[a]	6.2	9.1	15.3	Southern Baltic Sea	16	Ahlgren et al. (2005)
Euphausia superba (Euphausiacea)[b]	1.6	0.6	2.6	South Georgia, South Atlantic	20	Cripps et al. (1999)
Mysis mixta (Mysidacea)	13.7	9.5	23.2	Conception Bay, Newfoundland	174	Richoux et al. (2005)
Acanthostepheia malmgreni (Amphipoda)	8.7	5.7	14.4	Conception Bay, Newfoundland	119	Richoux et al. (2005)
Shellfish (12 species of Gastropoda and Bivalvia)	12.9	17.6	30.5	South Korea	81	Surh et al. (2003)
Brittle star *Amphiura elandiformis*	0.23	0.02	0.25	Southern Tasmania	2	Mansour et al. (2005)
Fish						
Cod (*Gadus morhua maris-albi*)	3.1	7.6	10.7	White Sea, north west of Russia	3	Gladyshev et al. (2007)
Gilthead sea bream (*Sparus aurata*)[c]	3.6	8.3	11.9	Mediterranean coast of Turkey	12	Ozyurt et al. (2005)
Herring (*Clupea harengus pallasi*)	5.6	12.3	17.9	Pacific Ocean, far east of Russia	3	Gladyshev et al. (2007)
Rock sole (*Lepidopsetta bilineata*)	7.2	4.6	11.8	Pacific Ocean, far east of Russia	3	Gladyshev et al. (2007)
Sea bass (*Dicentrarchus labrax*)[d]	7.5	14.2	21.7	Iskenderun bay, Mediterranean	48	Ozyurt and Polat (2006)
White sea bream (*Diplodus sargus*)[c]	4.4	10.2	14.6	Mediterranean coast of Turkey	9	Ozyurt et al. (2005)
Average for animals			15.4			

nr not reported

[a]Recalculated from Fig. 5 of the reference, using for copepods 1 g C = 2.75 g dry mass (from Alimov 1989) – see above table for zooplankton

[b]Recalculated from Tables 3 and 4 of the reference, using moisture content 10% (Alimov 1989)

[c]Recalculated from Tables 1 and 4 of the reference

[d]Recalculated from Tables 1 and 4 of the reference

that the average values will vary by more than a factor of 3 from the estimate presented here.

For freshwater zoobenthos we report data from four locations (Table 8.2) with an EPA + DHA average of 9.8 ± 1.6 mg g^{-1} DW. The number of HUFA measurements of zoobenthos species from diverse locations, like those of zooplankton, should be increased significantly in the future.

Data on HUFA content of freshwater fish from six locations are provided in Table 8.3. The average HUFA concentration is 8.1 ± 0.9 mg g^{-1} DW. Because of commercial interests the number of studies reporting HUFA concentrations in freshwater fish is higher than for zooplankton and zoobenthos (Tables 8.1 and 8.2) and, correspondingly, SE values are comparatively smaller. It is clear that data on HUFA content in as yet unmeasured freshwater fish species will still have to be obtained for more reliable generalizations.

In Table 8.4 very sparse data on HUFA content in only a few marine organisms are provided. The HUFA contents span two orders of magnitude, from 0.25 mg g^{-1} DW for the brittle star to 30.5 mg g^{-1} DW for shellfish (Table 8.4). Evidently, to calculate a more meaningful contribution of marine organisms to the global HUFA export, significantly more quantitative data are required. Furthermore, if one excludes humans, HUFA export from marine systems to terrestrial ecosystems would not reasonably be expected to include largely inaccessible deep water or open-water pelagic animals but would be restricted to marine organisms that inhabit the near-shore regions of marine and brackish systems.

In summary, one can readily see that comprehensive datasets on HUFA contents in groups of aquatic organisms are not yet available for the purposes of providing a more precise calculation of the global HUFA exports. Instead we will highlight some preliminary case studies for particular water-land HUFA fluxes.

8.5 Case Study I: Estimating the Export of Aquatic HUFA to Terrestrial Predators (Bears) in the Pacific Rim

The most conspicuous and well-documented aspect of terrestrial animals feeding on the aquatic organisms is the consumption of spawning Pacific salmon by terrestrial predators. This feeding represents an export of marine-derived energy and matter (and HUFA) to terrestrial ecosystems (Willson et al. 1998; Naiman et al. 2002; Helfield and Naiman 2006). Bears are believed to be the keystone consumer of these fish. It is necessary to emphasize that fish comprise a negligible part of bear rations outside of the area of Pacific Rim, where there are no anadromous salmon (e.g., Felicetti et al. 2004; Dobey et al. 2005). For example, in the vicinity of Yellowstone Lake consumption of cutthroat trout (*Oncorhynchus clarki*) by grizzly bears is ~18 kg trout $bear^{-1}$ $year^{-1}$ (Felicetti et al. 2004).

The average abundance of bears in the Pacific Rim is 0.19 ± 0.11 ind km^{-2}, and the average consumption of salmon by these bears is 416 ± 42 kg DW $bear^{-1}$ $year^{-1}$

(Table 8.5). Thus, bears convey to terrestrial ecosystems via consumption 79 kg DW km^{-2} $year^{-1}$ of aquatic productivity. Bears, on average, consume only ~50% of biomass of each salmon they kill (Willson et al. 1998; Gende et al. 2001; Reimchen 2000; Hilderbrand et al. 2004); the remaining parts of carcasses are included in terrestrial food webs via consumption by insects, birds, and small mammals. Thus, the total export of salmon biomass to terrestrial ecosystems can be estimated as $79 \times 2 = 158$ kg DW km^{-2} $year^{-1}$. It should be noted that the first line in Table 8.5 refers to measurements made at a location where the density of bears is known to be the highest in the world (southeastern Alaska), therefore adopting an average bear density 0.19 ind km^{-2} for the global calculations may lead to an overestimation of the export of salmon biomass by bears by a factor of 2.

Data on absolute EPA + DHA contents in Pacific salmon are very sparse. Gladyshev et al. (2006b) reported EPA and DHA concentrations of 0.536 ± 0.121 g 100 g^{-1} DW and 1.056 ± 0.152 g 100 g^{-1} DW, respectively, for humpback (pink) salmon (*Oncorhynchus gorbuscha*). Thus, the EPA + DHA concentration of pink salmon was, on average, 16.2 mg g^{-1} DW. This figure is close to that for land-locked rainbow trout (*O. mykiss*), given in Table 8.3 (Kainz et al. 2004). Using a salmon EPA + DHA concentration of 16 mg g^{-1} DW, we obtain a HUFA export to bears in terrestrial ecosystems of 2.5 kg km^{-2} $year^{-1}$. Although bears are the most visible consumers of salmon, they are not the only species to make use of this HUFA-rich food source. More than two dozen mammal and bird species are known to consume salmon carcasses especially in places where bears are relatively scarce (Szepanski et al. 1999; Darimont et al. 2003; Helfield and Naiman 2006). Thus, the total export of HUFA from Pacific salmon consumption by terrestrial predators and omnivores (bears and other animals consuming the remaining parts of carcasses) can be estimated to be ~5.0 kg DW km^{-2} $year^{-1}$.

Table 8.5 Abundance (*N*, ind. km^{-2}) of bears and their consumption of spawning salmon (*C,* kg DW $bear^{-1}$ $year^{-1}$)

Species	*N*	*C*	Region	References
Brown bear (*Ursus arctos*)	0.4	nr	Alexander Archipelago, Alaska	Ben-David et al. (2004)
Brown bear	0.15	nr	Wood River Lakes, Alaska	Helfield and Naiman (2006)
Grizzly bear (*Ursus arctos horribilis*)	0.03	391[a]	British Columbia	Hilderbrand et al. (2004)
Brown bear	nr	358[b]	Kenai Peninsula, Alaska	Hilderbrand et al. (1999b)
Black bear (*Ursus americanus*)	nr	498[a]	Haida Gwaii Islands, British Columbia	Reimchen (2000)
Average	0.19	416		

nr not reported

[a]Recalculated from wet weight using moisture content of salmon 71% (Winder et al. 2005)

[b]Recalculated from nitrogen consumption, using nitrogen content in fish 10% of DW (Vanni et al. 1997; Naiman et al. 2002)

Although we did not find quantitative estimates of the extent of spawning area in the available literature, we tried to estimate the global contribution of Pacific salmon to HUFA export to terrestrial ecosystems using the yearly oceanic production of Pacific salmon which migrate into rivers. The catch of Pacific salmon is used for the production estimation because exploitation rates are high, ranging from ~40 to 80% (Beamish et al. 1999). An average of the total catches (Canada, United States, Japan, and Russia) of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon in 1926–1995 can be obtained from Beamish et al. (1999; Fig. 6) as ~500 000 ton year^{-1}. Since the catches of these species account for about 90% of the total catch of all salmon species (Beamish et al. 1999), the total catch of Pacific salmon can be estimated at ~555,000 ton year^{-1}. Using the average exploitation rate (40 + 80)/2 = 60%, the annual biomass of salmon population migrating into rivers is estimated to yield 925,000 tons. On the basis of data of (Reimchen 2000; Quinn et al. 2003; Winder et al. 2005; Helfield and Naiman 2006) we estimated that bears, on average, kill ~47% of salmon spawning in rivers. The salmon die after spawning, but many of their carcasses stay within aquatic ecosystems. We take into account only those directly exported to terrestrial ecosystems. Thus, the total annual export of salmon to terrestrial ecosystems via bear predation is 434,000 ton wet weight (126,000 ton dry weight). Considering the HUFA content in pink salmon (~16 mg g^{-1} DW; Gladyshev et al. 2006b) as a proxy for other Pacific salmon, the annual HUFA export to terrestrial ecosystems via bear predation on Pacific salmon is estimated to be 2×10^6 kg year^{-1}. In the following we will try to compare the export of HUFA from aquatic ecosystems via bears with the other fluxes, such as insect emergence, bird feeding (Fig. 8.1), and human fisheries.

8.6 Case Study II: Humans and Fisheries

Humans, although not explicitly depicted in Fig. 8.1, are terrestrial predators that actively consume HUFA-rich resources from aquatic ecosystems. The total world catch (1998–2003; marine and freshwater) of fish and shellfish was ~92.2×10^6 ton year^{-1} (FAO 2004). Using the data in Tables 8.3 and 8.4, and assuming a moisture content of 80%, the average HUFA content in the captured wet biomass can be estimated as 2 mg g^{-1}. Thus, man withdraws from aquatic ecosystems ~1.8 10^8 kg year^{-1} of EPA + DHA. This number is ~90× higher than the HUFA export through bears hunting salmon in Pacific Rim. Human consumption of wild and farmed fish and aquatic invertebrates is ~16 kg per person per year (FAO 2004). This means that the global average personal daily consumption of EPA + DHA is about 0.1 g, i.e., about ten times lower than is currently recommended by the World Health Organization. Worldwide exploitation rates of fisheries have been shown to be too high, even at present (Pauly et al. 2002). Thus, the further development of aquaculture and/or genetic engineering, for example, the insertion of genes directing HUFA synthesis into terrestrial oil-seed producing plants, may be required to supply mankind with the appropriate quantity of essential HUFA in order to avoid overexploiting natural aquatic ecosystems in the future (see also Chap. 9).

8.7 Case Study III: Estimation of the Export of HUFA Through Aquatic Insect Emergence

The emergence of aquatic insects is one of nature's most conspicuous displays of the export of aquatic-derived biomass to the terrestrial landscape. Insects from the orders Ephemeroptera (mayflies), Diptera (midges, black flies), Trichoptera (caddisflies), Plecoptera (stoneflies) lay their eggs in rivers, ponds, and lakes where the larvae then develop and accumulate HUFA throughout the various larval stages until they emerge as adults and enter the riparian zone and adjacent regions where mating occurs. In productive environments this emergence can be so prodigious that it can readily be detected by land-based radar, a tool with the potential to reveal both spatial and temporal variations in the strength of insect emergence (Fig. 8.3).

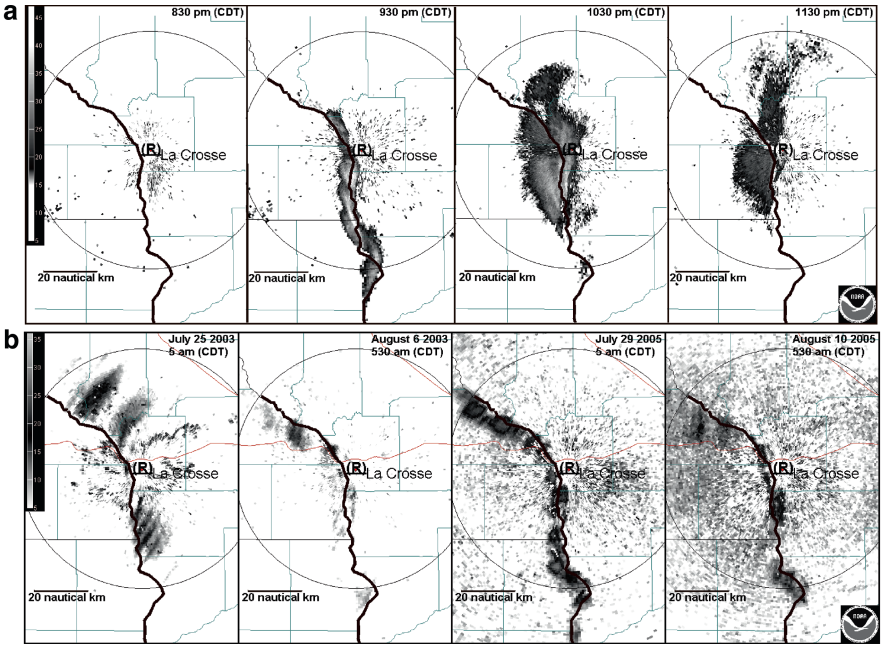

Fig. 8.3 Mayfly (Ephemeroptera) hatches from the Mississippi River centered on the city of La Crosse, Wisconsin, USA, as captured by radar images taken by the National Weather Service Office, National Oceanographic and Atmospheric Administration, La Crosse, Wisconsin. Evolution of the mayfly hatch: (**a**) during the evening of June 30, 2006; wind from the south, and (**b**) on, from left to right, July 25, 2003; August 6, 2003; July 29, 2005; and August 10, 2005 with accompanying wind directions of; SW, NE, NE, and NE, respectively. The decibels that are returned are energy returned which is a function of density and target dimensions. Since the same target dimensions are roughly the same (although the mayfly bodies are randomly oriented to the beam), the scale on the left of each figure provides a measure of relative insect density. The circle (ring) indicates where the radar beam, originating at (*R* radar source) and emanating away at an angle of 0.5° above the surface, reaches 1 km above the river valley floor. With radar, a greater distance away from the radar indicates a greater elevation of the echo

Emergence of aquatic insects, calculated from diverse literature data (Table 8.6), is, on average, 4.1 ± 1.9 g DW m^{-2} $year^{-1}$. Our calculations give the same value as an independent global estimate made by Baxter et al. (2005). Variations of the emergence value in diverse ecosystems were from 0.2 to 23.1 g DW m^{-2} $year^{-1}$, i.e., spanning two orders of magnitude. The return of aquatic adults to streams was estimated at ~1.5% of the emergence (Ballinger and Lake 2006). Therefore, the net export of biomass of emergent aquatic insect can be estimated as ~4.3 g DW m^{-2} $year^{-1}$. To calculate the export of HUFA, we need to know the EPA and DHA content of the imagoes of aquatic insects. Such data are not common in the available literature. Nevertheless, we had, available to us, one sample of the imago of chironomids collected near the site where we studied zoobenthos (Sushchik et al. 2003). Concentrations of EPA and DHA in these imagoes were 17.8 mg g^{-1} DW and 0.3 mg g^{-1} DW, respectively, using a moisture content of 72% (see footnote to Table 8.2). The sum of these two values was of the same order of magnitude as the average HUFA (EPA + DHA) content in the larvae of aquatic insects, 9.3 ± 2.2 mg g^{-1} DW (Table 8.2).

Table 8.6 Aquatic insect emergence, g DW m^{-2} $year^{-1}$, from diverse ecosystems

Dominant taxa	Emergence	Ecosystem, Region	References
Diptera, Ephemeroptera, Plecoptera, Odonata	4.5	Global generalization	Baxter et al. (2005)
Ephemeroptera, Plecoptera, Trichoptera	0.382	Pick Creek, southwestern Alaska	Francis et al. (2006)
Chironomidae (>50%)	2.1[a]	Rivers of Philippines island	Freitag (2004)
Many taxa	10[b]	Global generalization	Huryn and Wallace (2000)
Chironomidae	1.1[a]	Temporary wetland pond, South Carolina	Leeper and Taylor (1998)
Chironomidae	0.2[a]	Salt marsh, southern Maine	MacKenzie (2005)
Odonata, Ephemeroptera	0.5	Lake Michigan coastal wetland	MacKenzie and Kaster (2004)
Many taxa	1.2[c]	Stream, Hokkaido, Japan	Nakano and Murakami (2001)
Plecoptera, Ephemeroptera, Chironomidae	6.3	Tagliamento River (NE-Italy)	Paetzold et al. (2005)
Diptera, Trichoptera, Ephemeroptera	1.7	Outlet of Lake Belau, Germany	Poepperl (2000)
Chironomidae, Trichoptera	23.1	Sycamore Creek, Arizona	Sanzone et al. (2003)
Chironomidae	1.5	Wetland in Alabama	Stagliano et al. (1998)
Many taxa	1.3[d]	Lake Esrom, Denmark	Woollhead (1994)
Average	4.1		

[a]Recalculated using an average specimen dry mass of 150 μg (Stagliano et al. 1998)
[b]Recalculated from aquatic insect production
[c]Recalculated form Fig. 1C of the reference
[d]Recalculated using energy equivalent 1 g DM = 23 kJ (Alimov 1989)

Therefore, we make the assumption that mean EPA and DHA concentration of emerging insects is roughly equal to that in their aquatic larvae. Using the average HUFA concentration in larvae of aquatic insects (i.e., 9.3 mg g^{-1} DW), the export via emerging aquatic insects can be estimated as 4.3 × 9 = 40 mg m^{-2} (kg km^{-2}) $year^{-1}$.

The two orders of magnitude difference in the reported emergence values among different ecosystems and the paucity of data on HUFA content in imagoes mean that our first-ever estimates of HUFA export from aquatic to terrestrial systems should be regarded as very coarse. Using the lowest and highest values (worst- and best-case scenarios) of insect larvae HUFA contents (Table 8.2) and those of emergence (Table 8.6) we may suppose that, for the particular ecosystems cited here, the HUFA export values can vary from as little as 0.1 mg m^{-2} $year^{-1}$ to as high as 672.2 mg m^{-2} $year^{-1}$. Clearly, more studies reporting on the abundance and HUFA content of larval insects from riverine and wetland environments as well as the emergence densities of adult forms are necessary in order to calculate a more reliable estimate of the contribution that emerging insects make to the export of HUFA from aquatic to terrestrial ecosystems.

8.8 Case Study IV: Estimation of Aquatic HUFA Import to Terrestrial Ecosystems Through Birds

Birds import a significant amount of aquatic HUFA to terrestrial ecosystems. While ducks, loons, mergansers, etc. clearly fall into the category of "water birds" there are other birds that are usually thought of as "terrestrial" but which, depending on the season, do consume a large number of aquatic organisms. For example, swallows (Hirundinidae) consume great quantities of mosquitoes, black flies, mayflies, and caddisflies during peak insect emergence periods. Many other terrestrial birds, e.g., songbirds, rely to varying extents on the emergence of insects from aquatic systems. Finally, HUFA-rich amphipods which are often abundant in littoral areas of lakes and in ponds may become infected with acanthocephalan parasites causing a well-described positive phototaxis (Benesh et al. 2005). This infection, in turn, makes them more widely susceptible to predation by shorebirds such as terns (Sternidae) and sandpipers (Scolopacidae).

Water bird abundance (biomass) depends on lake trophic status and morphometry, i.e., surface area, shoreline length (e.g., Hoyer and Canfield 1994; Suter 1994). Nevertheless, by generalizing data from diverse water bodies and locations (Table 8.7), one can see that annual abundances are very close to each other and on average can be estimated as ~0.4 ± 0.1 ind 10^{-3} m^{-2}.

The energy content of aquatic organisms, consumed by an "average" bird (mean individual weight = ~0.7 kg) from a community with 19 different species, can be estimated from the data of Gardarsson and Einarsson (2002) as 227,000 kJ $ind.^{-1}$ $year^{-1}$. The 1 g DW = 23 kJ conversion factor provided by Alimov (1989) yields an annual intake of aquatic organisms by the "average bird" of 9.9 kg DW $ind.^{-1}$ $year^{-1}$.

Table 8.7 Abundance (*N*, ind. × 10^{-3} m^{-2}) of water birds in diverse ecosystems and their consumption of aquatic invertebrates and fish (*C*, g m^{-2} $year^{-1}$ dry mass)

Dominant taxa (number of species)	*N*	*C*	Ecosystem, Region	References
Pelicans, cormorants, herons, royal tern (23)	0.4	10.4[a]	Lagoon on the Pacific Coast of Mexico	Acuna et al. (1994)
Ducks *Anas* spp. (4)	0.7[b]	18.2[a]	Boundary Bay, British Columbia, Canada	Baldwin and Lovvorn (1994)
Tufted ducks, greater scaup, merganser (19)	0.5	4.9	Lake Myvatn, Iceland	Gardarsson and Einarsson (2002)
Mallard, coot, red-winged blackbird (50)	0.2	5.2[a]	46 Florida lakes	Hoyer and Canfield (1994)
Mallard, cormorant (not reported)	0.1[c]	2.6[a]	Lake Grand-Lieu, France	Marion et al. (1994)
Anas platyrhynchos, Aythya fuligula (63)	0.25	6.5[a]	158 fishponds, Bohemia, Czech Republic	Musil and Fuchs (1994)
Anser, *Aythya* (7)	0.7[d]	18.2[a]	Lake Balaton, Hungary	Ponyi (1994)
Tufted duck, coot, mallard, pochard (29)	0.1[e]	2.6[a]	20 major Swiss lakes, north of the Alps	Suter (1994)
Anas, *Aythya*, *Fulica*, *Cygnus*, *Podiceps* (26)	nr	2.1	Lake Esrom and Lake Sjelso, Denmark	Woollhead (1994)
Average	0.4	7.8		

nr not reported
[a]Calculated using *N* and the intake of aquatic organisms by the "average" bird, 26 kg DM $ind.^{-1}$ $year^{-1}$ (see text for details)
[b]Estimated from Fig. 2 of the reference.
[c]Calculated from Table 1 of the reference (only birds, feeding in the lake)
[d]Calculated from Table 4 of the reference
[e]Estimated from Fig. 2 of the reference

On the basis of data from Gere and Andrikovics (1994) for ducks from Lake Balaton, Hungary, intake can be estimated as 43 kg DW $ind.^{-1}$ $year^{-1}$. Thus, for the following calculation, we use the mean value obtained from these two estimates, i.e., 26 kg DW $ind.^{-1}$ $year^{-1}$. It is important to note that average individual bird biomass, calculated on the basis of data from 46 Florida lakes where the bird community comprised 50 species, was 0.6 kg (Hoyer and Canfield 1994), i.e., similar to the value given earlier. Thus, our calculations of intake, based on the "average" bird at ~0.7 kg, seem reasonable for many ecosystems. On average then, the annual consumption of aquatic animals by water birds is 7.8 g ± 2.1 DW m^{-2} $year^{-1}$ (Table 8.7).

Using an average EPA + DHA content for aquatic animals of 9.2 mg g^{-1} DW (calculated from Tables 8.1–8.3) the HUFA export from a "typical" aquatic ecosystem by water birds can be estimated as ~7.8 × 9.2 ≈ 72 kg km^{-2} $year^{-1}$. Based on the observed variation in this preliminary dataset, global HUFA export rates can be expected to range anywhere from 19.3 to 167.4 kg km^{-2} $year^{-1}$. These values, although imprecise, provide some idea of the scale of HUFA export from aquatic systems to aquatic or riparian birds.

8.9 Case Study V: Can HUFA Export from Aquatic Ecosystems Meet the HUFA Requirements of Terrestrial Animals?

Using available data, we carry out the first calculations of HUFA export from selected aquatic to terrestrial ecosystems. We suggest that, except for particular locations in the Pacific Rim where bears intensively consume salmon, the main pathways of HUFA export are emerging insects and water birds. It is also likely that, in some ecosystems, emerging amphibians can make a substantial contribution to the HUFA export. However, we failed to find in the available literature the necessary quantitative data on amphibian abundance, biomass, emergence, and HUFA content. We measured the EPA + DHA content in two specimens of frog (*Rana ridibunda*) (Palla) caught in the vicinity of Krasnoyarsk city (Siberia, Russia) and obtained a value of 2.0 mg g^{-1} DW. The content of essential HUFA in these amphibians is lower than in many fish and aquatic invertebrates (Tables 8.1–8.3), but nonetheless significant.

Hence, at present we will for the following considerations only use the HUFA export rates due to emerging insects and water birds. As mentioned earlier, to correlate HUFA export with the requirements of terrestrial animals one must know, besides the fluxes (i.e., g of HUFA m^{-2} $year^{-1}$), the area of the adjacent terrestrial ecosystem, metabolic HUFA requirements of carnivorous and omnivorous terrestrial animals and their biomass. At present no detailed comprehensive studies have been conducted with these specific parameter estimates. Nevertheless, since we here have estimated the first coarse average figures (Tables 8.1–8.7) it is very tempting to carry out some calculations for an "average" ecosystem. Since there are no available relevant data for any particular ecosystem, we decided to approach the task from the other side and model an "average" ecosystem using available global-scale data.

8.9.1 Area of Terrestrial Ecosystems and Inland Aquatic Ecosystems and Average HUFA Export

First, we need to develop a relationship between terrestrial and aquatic ecosystem areas. The total landmass area of terrestrial ecosystems has been estimated at 99.5 $\times 10^6$ km^2 (Alimov 1989). In comparison, the total area of large lakes and rivers has been estimated at 2.0×10^6 km^2 (Alimov 1989; Raven and Maberly 2004). The number of small waterbodies (0.1–1.0 ha), characteristic of wetlands in subarctic regions for example, is large and has been estimated at between 5×10^8 and 8×10^7 (Wetzel 1992) providing a vast surface area of 20×10^6 km^2 (upper limit). Therefore, by including waterbodies with a surface area between 0.001 and 1 km^2 the total landlocked waterbody area can be estimated as ~22×10^6 km^2. Subtracting the surface area of small lakes (1 km^2 and less, i.e., 20×10^6 km^2) yields a net landmass area of

terrestrial ecosystems of 79.5 × 10^6 km^2. Because of their physical proximity and connectivity with terrestrial systems we also include the surface area of estuaries, i.e., 1.4 × 10^6 km^2 (Alimov 1989; Raven and Maberly 2004) in our calculations and adding it to the total area of inland waters. Hence, the total surface area of aquatic ecosystems, i.e., freshwater and estuaries, which can potentially supply terrestrial ecosystems with HUFA, is 23.4 × 10^6 km^2. Thus, on a surface area basis, production of HUFA from 1 m^2 of such model inland aquatic ecosystems (lakes, rivers and estuaries) can potentially supply 3.4 m^2 (i.e., 79.5/23.4) of terrestrial ecosystems.

One recent calculation (Downing et al. 2006) provides a contrasting estimate of total inland water area of ~4.6 × 10^6 km^2. Although there might be some underestimation, e.g., too low of a predicted density of small waterbodies in tundra regions, we will use the Downing et al. figure as our "lower limit" estimate. Therefore, by subtracting the additional surface area of lakes, 2.6 × 10^6 km^2, calculated in the study, cited earlier, from the total landmass area we get a net landmass area of terrestrial ecosystems of ~96.9 × 10^6 km^2. The lower limit of total surface area of aquatic ecosystems, which can potentially supply terrestrial ecosystems with HUFA, is 4.6 × 10^6 km^2 + 1.4 × 10^6 km^2 (estuaries) = 6.0 × 10^6 km^2. Thus, according to the lower limit estimate, production of HUFA from 1 m^2 of possible inland aquatic ecosystems supplies 96.9 × 10^6/6.0 × 10^6 = 16.2 m^2 of terrestrial ecosystems. Therefore, for all the following calculations, which refer to the area of aquatic ecosystems, the lower limit estimate will be 3.9× lower (i.e., 23.4 × 10^6 km^2/6.0 × 10^6 km^2) than the upper limit estimate. For the ratio between areas of terrestrial and aquatic ecosystems, the lower limit estimate yields a 4.8× lower value (i.e., 16.2 m^2/3.4 m^2 of terrestrial ecosystems supplied with HUFA from 1 m^2 of aquatic ecosystems).

Thus, 1 m^2 of surface area of the model "average" aquatic ecosystem can potentially provide HUFA to between 3.4 and 16.2 m^2 of the model "average" adjacent terrestrial ecosystem. The sum of the average values of the two HUFA fluxes through emerging insects and water birds, calculated earlier, is 40 + 72 = 112 mg m^{-2} (kg km^{-2}) $year^{-1}$. Therefore, HUFA supply to the model "average" terrestrial ecosystem can be from 6.9 to 32.9 kg km^{-2} $year^{-1}$. The HUFA supply due to emerging insects, which will be used for the following case study, ranges from a low of 2.5 to a high of 11.8 kg km^{-2} $year^{-1}$.

8.9.2 Relation of HUFA Export to Biomass of Terrestrial Animals

In Sect. 8.4 we attempted to relate HUFA supply to the requirements of the human population and found that a potentially significant deficiency exists with respect to the continued supply of essential fatty acids to humans. Next we try to answer a similar question: is the HUFA export from the model "average" aquatic ecosystem high enough to support terrestrial animals, which we suggest must also, to varying degrees, obtain HUFA from their food? To answer this question, we need to know the average metabolic requirements and biomass of omnivorous and carnivorous terrestrial animals in the "average" model terrestrial ecosystem.

We take into consideration secondary consumers only. Herbivorous animals, e.g., ruminants, hardly consume the production of aquatic ecosystems, and more likely obtain HUFA from their precursor ALA which is quantitatively abundant in higher plants, or through synthesis by symbiotic intestinal micro-organisms. Although gut microbes are an additional potential source of HUFA, very little is known of the overall importance of this source (Hulbert et al. 2002).

Next we need to obtain an estimate of the average HUFA requirements for omnivorous and carnivorous terrestrial animals. The requirements for humans are in the range of 180–1,000 mg person^{-1} d^{-1} (Garg et al. 2006). If we use 70 kg as an average weight of a human, the HUFA requirements may be expressed as 2.6–14.3 mg kg^{-1} WW d^{-1}, or, on average, ~8 mg kg^{-1} WW d^{-1}. Data on HUFA requirements for animals are very sparse in the available literature. A daily supplementation of EPA + DHA of 22 mg kg^{-1} WW d^{-1} for dogs with early stages atopy gave a good clinical effect (Abba et al. 2005). For rats, a diet with a HUFA intake of 0.6 mg g^{-1} WW d^{-1} (600 mg kg^{-1} WW d^{-1}) was found to be most advantageous to long bone density (Green et al. 2004).

For the case study we choose omnivorous rodents, assuming that they have HUFA requirements, close to that of rat, mentioned earlier. One widespread and comparatively well-studied species is the deer mouse (*Peromyscus maniculatus*). It has an average individual biomass of ~17 g WW (Merritt et al. 2001; Stapp and Polis 2003), and insects are a staple in their diet (Merritt et al. 2001). Their densities ranged from 1.0 to 13 ind. ha^{-1} in prairie of Central Plains, Colorado, USA (Stapp and Van Horne 1997), to 9.0–16.9 ind. ha^{-1} in forests of west-central British Columbia (Sullivan et al. 1999) and to 1.0–17.6 ind. ha^{-1} in the Kananaskis Valley, southwestern Alberta, Canada (Millar and McAdam 2001). Thus, the average biomass of these mice in diverse ecosystems ranged from 17 to 299.2 g ha^{-1} or from 1.7 to 29.9 kg km^{-2}. HUFA (EPA + DHA) requirements of these rodents, using the earlier assumption, ranged from 1.0 g km^{-2} d^{-1} to 17.9 g km^{-2} d^{-1}, or 0.37–6.53 kg km^{-2} year^{-1}. The supply of HUFA due to emerging insects, which contribute to the food items of these mice, from the "average" aquatic to the "average" terrestrial ecosystem, calculated earlier, is from 2.5 to 11.8 kg km^{-2} year^{-1}. Thus, according to these extremely simplified considerations, there exists at least the potential for situations in which there may be a shortage of HUFA in deer mice populations. Clearly, more focused research is needed to ascertain the contributions and effects of aquatic versus terrestrially derived HUFA in deer mice population dynamics. It is an equally valid question to ask if other omnivorous and carnivorous terrestrial animals, besides deer mice, also depend, to various extents, on aquatic-source-derived HUFA.

8.10 Ocean Contribution

Biomass from marine ecosystems enters the coastal-terrestrial ecosystems through shore drift of algal wrack and carrion (Polis and Hurd 1996). There are many terrestrial consumers of such marine-derived inputs: spiders, scorpions, ants, lizards,

landbirds, coyotes, foxes, jackals, etc. (Polis and Hurd 1996). In marine islands there are also deer mice, described in the case study in Sect. 8.7.2., which consume littoral detritus (Stapp and Polis 2003).

Polis and Hurd (1996) estimated that the average dry mass of algal drift arriving per linear meter of supralittoral was 27.6 kg m^{-1} $year^{-1}$. A large quantity of algae washes ashore as a consequence of either storms or seasonal mortality and breakup of algal beds. Using the data of Fleurence et al. (1994; Table 8.4) on the HUFA content of seaweeds, 1.3 mg g^{-1} DW, import of EPA + DHA through the shore drift to a coastal ecosystem could be as high as 36 g m^{-1} $year^{-1}$.

Carrion drift, estimated from the data of Polis and Hurd (1996), is 0.3 kg DW m^{-1} $year^{-1}$. Using the average content of EPA + DHA in marine animals (Table 8.4), the HUFA export to a coastal terrestrial ecosystem could be ~5 g m^{-1} $year^{-1}$, and thus total export through the shore drift (plants + animals) is 36 + 5 = 41 g m^{-1} $year^{-1}$. This input of HUFA to terrestrial ecosystems is evidently very important for local coastal areas, especially for small islands. Unfortunately, there are no quantitative data for any particular ecosystem on the biomass of terrestrial animals, which consume the drift products and therefore, at present, we can say very little about the HUFA deficiency potential for coastal ecosystems.

In order to compare export of HUFA from the oceanic drift contribution with those from inland waters we need to use a coarse, global-scale analysis. The total linear distance of global coastlines has been estimated as 594,000 km (Polis and Hurd 1996). Thus, global HUFA export from the drift, estimated in the case study of Polis and Hurd (1996) in conjunction with the average HUFA content of marine organisms (Table 8.4), may be ~24×10^6 kg $year^{-1}$. If we use the surface area estimate of inland waters and estuaries as 23.4×10^6 km^2 and the average HUFA export through emerging insects and birds as 112 kg km^{-2} $year^{-1}$ (see Sect. 8.7.1), then the global HUFA export from the inland waters appears to be ~3×10^9 kg $year^{-1}$. Thus, the ocean contribution to the global HUFA export could be ~100 times lower than that of inland waters. The cause of this phenomenon is the comparatively higher amount of interface (ecotone zone) between inland waters and terrestrial ecosystems. Indeed, if we take into consideration lakes with a surface area of 1 ha (0.01 km^2) the perimeter of each lake would be at least 0.35 km ($L = 2\pi r = 0.35$ km), if one equates their shape to a circle. The number of such lakes, as mentioned in Sect. 8.7.1, is ~1×10^8 (Wetzel 1992); thus, their total perimeter is 35×10^6 km. If one were to add the shoreline of large lakes the total perimeter of inland waters will be at least twice as high (~70×10^6 km). This figure is much larger than the length of ocean shoreline (~0.6×10^6 km). Thus, it is not surprising that the interaction between inland waters and terrestrial ecosystems is much higher than that between the ocean and terrestrial ecosystems. It is interesting to note that if one relates the estimated HUFA export from the perimeters (shores) of inland waters (i.e., 3×10^9 kg $year^{-1}/70 \times 10^6$ km = 43 g m^{-1} $year^{-1}$) the resulting estimate is very similar to the HUFA export estimated to be due to the contribution from ocean shoreline perimeters (41 g m^{-1} $year^{-1}$).

8.11 Assumptions and Underestimates

Our attempt to calculate HUFA export from aquatic to terrestrial ecosystems is the first one, and obviously there are many underestimates caused, in part, by an absence of relevant data in the available literature (see Sect. 8.1). First, we could not calculate the export of HUFA through amphibian emergence. In some ecosystems amphibians are very abundant, and their contribution to food webs is quantitatively important (Burton and Likens 1975; Ballinger and Lake 2006).

Second, we took into consideration only consumption of salmon by bears around the Pacific Rim. However, there are many other terrestrial "interface specialists" – primary and secondary consumers, such as beetles, spiders, lizards, etc., which scavenge aquatic organisms, washed up on the banks, as well as large mobile mammals, such as the hippopotamus which are important conduits for energy exchange across the aquatic – terrestrial interface in some regions (Ballinger and Lake 2006). Third, for inland waters we do not take into account flooding and drying events which also directly subsidize terrestrial ecosystems with fresh biomass of aquatic organisms (Ballinger and Lake 2006). Fourth, we omitted colonies of seabirds on rocks and shelf ice. Thus, our conclusion about possible limitation of the "average" terrestrial ecosystem with HUFA export from the adjacent "average" aquatic ecosystem may be underestimating the true potential for limitation for many ecosystems. However, it is also clear that there are very little available data (with the exception of some commonly studied species such as rats, dogs, and cats) on the innate ability of terrestrial animals to desaturate and elongate ALA to EPA and DHA. This ability, if present at a reasonably ubiquitous level in terrestrial organisms and/or their symbiotic microbial gut communities, would have the opposite effect on our estimates of the potential for HUFA limitation in terrestrial systems. Clearly much more work needs to be done.

8.12 Conclusions and Perspectives

According to our coarse average estimations at least some components of terrestrial ecosystems have the potential to be limited by the supply of essential HUFA from adjacent aquatic ecosystems. On a global scale it seems reasonable to conclude that the main flux of aquatic HUFA to terrestrial ecosystems (excluding humans) originates from inland waters and estuaries, rather than from the ocean. Nevertheless, our estimate of HUFA fluxes are inevitably coarse because detailed data on HUFA synthesis, transfer, and retention in organisms at the water-land interface are scarce and limited to incomplete studies conducted in only a few ecosystems. Thus, we suggest that future studies should be aimed at obtaining more comprehensive quantitative estimates of (a) specific fluxes of HUFA from particular aquatic ecosystems to surrounding terrestrial ecosystems, (b) abilities of terrestrial organisms to

synthesize n-3 HUFA (from ALA), and (c) level of HUFA required from the diet in order to maintain optimal physiological performance.

It is likely that in different types of biomes (e.g., tundra, taiga, rain forests, savanna, steppe, deserts, etc.) there are different ecological roles in the context of HUFA export and that some terrestrial ecosystems may be more limited than others by the quantity of essential HUFA exported from adjacent aquatic ecosystems. Moreover, the role of anthropogenic pollution and/or climate change in affecting aquatic HUFA production and export and hence the functioning of terrestrial ecosystems (from the perspective of creating potential HUFA deficiencies) should be investigated.

Aquatic ecologists today are faced with global challenges and must integrate knowledge from a variety of disciplines. One such challenge involves quantifying the production, storage, and movements of HUFA in aquatic ecosystems of different types leading to better estimates of their contribution to the health and ecological integrity of aquatic and terrestrial ecosystems. A particularly important task is to estimate the potential role of different organisms and aquatic ecosystems as sources and sinks of healthy, biochemically valuable food for human nutrition. This is critical in that the consumption of the n-3 HUFA by humans is suspected as being insufficient even in Western developed countries (see Chap. 14). Current evidence from nutritional, epidemiological, and clinical studies shows that a regular shortage of n-3 HUFA in the diet aggravates cardiovascular diseases in humans and may limit normal neonatal and infant brain growth and perhaps intellectual development (see Chap. 14). However, such studies should be well grounded/founded on a detailed knowledge of fatty acid contents in natural fish and aquatic invertebrate populations in relation to the taxonomic affiliation, trophic position, age, and diet of the main contributing species. The HUFA accumulation and transfer rates within food webs should be traced and measured leading to better estimates of the potential total harvest of HUFA in different aquatic ecosystems. HUFA are also very important to the aquaculture industry which face the constant challenge of maintaining adequate concentrations of essential fatty acids in the diets of cultured organisms (e.g., Atlantic salmon, shrimp). This is because overfishing for forage fish is rapidly increasing the cost, and simultaneously threatening to decrease the quality, of fish-meal-based feeds (see Chap. 9).

Second, potential hazards which may reduce HUFA production must be studied, forecasted, and, where possible, mitigated. For instance, we postulate that anthropogenically induced processes such as eutrophication and global climate change (see Chap. 11) may, either qualitatively or quantitatively (or both), lead to decreased HUFA production and storage in aquatic ecosystems. This is because: (a) eutrophication in aquatic ecosystems favors cyanobacteria (blue-green algae) which often contain very little, if any, HUFA (see Chap. 7) and, (b) warmer temperatures have the general effect of reducing the concentrations of long-chain fatty acids such as EPA and DHA in biomembranes in a wide range of aquatic organisms (see Chap. 10; Schlechtriem et al. 2006). Such threats coupled with the critical need for these substances in animal and human diets underline the urgency of this new direction of research on HUFA fluxes. Given the importance of essential fatty acids for animal

and human health and nutrition and for existing and emerging aquaculture facilities, follow-up studies are necessary in order to more precisely identify the sources' sinks and flows of these compounds as well as to characterize the risks to their continued production.

In summary, to further improve the component estimates required for a more reliable world-wide estimate we suggest that the following quantitative studies are required: (1) insect emergence in conjunction with HUFA measurements in their biomass, (2) water bird abundance and ration, including HUFA content of their food, (3) amphibian emergence and contents of HUFA in their biomass, (4) abundance and ration of riparian animals, including HUFA content of the portion of their food obtained from water, (5) abundance and ration of terrestrial predators, consuming emergent insects, amphibians and water birds, and (6) HUFA requirements of diverse terrestrial animals. The studies, proposed earlier, should be carried out in diverse aquatic ecosystems, pools, swamps, lakes, rivers, seas, situated in different landscapes: tundra, taiga, steppe, mountains, desert, etc. Additional and more precise estimates of the surface area of aquatic ecosystems and adjacent terrestrial ecosystems are also essential.

Finally, it is now well recognized that, beyond the obvious provisioning of drinking water, navigation, and flood control, aquatic ecosystems provide a variety of additional and highly valuable "ecosystem services." These include esthetic and recreational services as well as their recently recognized role in mitigating the effects of a wide variety of organic contaminants. To this list of services we must now add one heretofore unrecognized service, namely, the provision of essential HUFA to adjacent terrestrial systems. This newly recognized service of aquatic ecosystems provides conservationists and resource managers with a new outlook and justification for preserving lakes, rivers and wetlands.

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References

Abba, C., Mussa, P.P., Vercelli, A. and Raviri, G. 2005. Essential fatty acids supplementation in different-stage atopic dogs fed on a controlled diet. J. Anim. Physiol. Anim. Nutr. 89:203–207

Acuna, R., Contreras, F. and Kerekes, J. 1994. Aquatic bird densities in two coastal lagoon systems in Chiapas State, Mexico, a preliminary assessment. Hydrobiologia. 279/280:101–106

Ahlgren, G., Blomqvist, P., Boberg, M. and Gustafsson, I.-B. 1994. Fatty acid content of the dorsal muscle – an indicator of fat quality in freshwater fish. J. Fish Biol. 45:131–157

Ahlgren, G., Carlstein, M. and Gustafsson, I.-B. 1999. Effects of natural and commercial diets on the fatty acid content of European grayling. J. Fish. Biol. 55:1142–1155

Ahlgren, G., Ahlgren, I., Hernandez, S. and Mejia, M. 2002. Fatty acid quality of seston in the Lakes Xolotlan and Cocibolca, Nicaragua. Verh. Internat. Verein. Limnol. 28:786–791

Ahlgren, G., Van Nieuwerburgh, L., Wanstrand, I., Pedersen, M., Boberg, M. and Snoeijs, P. 2005. Imbalance of fatty acids in the base of the Baltic Sea food web – a mesocosm study. Can. J. Fish. Aquat. Sci. 62:2240–2253

Aktas, H. and Halperin, J.A. 2004. Translational regulation of gene expression by ω-3 fatty acids. J. Nutr. 134:2487S–2491S

Alimov, A.F. 1989. An Introduction to Production Hydrobiology. Leningrad: Gidrometeoizdat (in Russian). 152 pgs

Arts, M.T., Ackman, R.G. and Holub, B.J. 2001. "Essential fatty acids" in aquatic ecosystems: a crucial link between diet and human health and evolution. Can. J. Fish. Aquat. Sci. 58:122–137

Baldwin, J.R. and Lovvorn, J.R. 1994. Habitats and tidal accessibility of the marine foods of dabbling ducks and brant in Boundary Bay, British Columbia. Mar. Biol. 120:627–638

Ballinger, A. and Lake, P.S. 2006. Energy and nutrient fluxes from rivers and streams into terrestrial food webs. Mar. Freshw. Res. 57:15–28

Baxter, C.V., Fausch, K.D. and Saunders, W.C. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshw. Biol. 50:201–220

Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V. and Kurashov, V. 1999. The regime concept and natural trends in the production of Pacific salmon. Can. J. Fish. Aquat. Sci. 56:516–526

Ben-David, M., Titus, K. and Beier, L.R. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? Oecologia 138:465–474

Benesh, D.P., Duclos, L.M. and Nichol, B.B. 2005. The behavioral response of amphipods harboring *Corynosoma constrictum* (acanthocephala) to various components of light. J. Parasitol. 91:731–736

Blair, T.A., Cree, A. and Skeaff, C.M. 2000. Plasma fatty acids, triacylglycerol and cholesterol of the tuatara (*Sphenodon punctatus punctatus*) from islands differing in the presence of rats and the abundance of seabirds. J. Zool. 252:463–472

Boersma, M. and Kreutzer, C. 2002. Life at the edge: is food quality really of minor importance at low quantities? Ecology 83:2552–2561

Broadhurst, C.L., Wang, Y., Crawford, M.A., Cunnane, S.C., Parkington, J.E. and Schmidt, W.F. 2002. Brain-specific lipids from marine, lacustrine, or terrestrial food resources: potential impact on early African *Homo sapiens*. Comp. Biochem. Physiol. B. 131:653–673

Burton, T.M. and Likens, G.E. 1975. Energy flow and nutrient cycling in salamander population in the Hubbard Brook experimental forest, New Hampshire. Ecology. 56:1068–1080

Cohen, Z., Norman, H.A. and Heimer, Y.M. 1995. Microalgae as a source of ω3 fatty acids. In: Plants in human nutrition. World review of nutrition and dietetics, Vol. 77. Edited by Simopoulos, A.P. Basel: Karger, pp. 1–31

Copeman, L.A., Parrish, C.C., Brown, J.A. and Harel, M. 2002. Effects of docosahexaenoic, eicosapentaenoic, and arachidonic acids on the early growth, survival, lipid composition and pigmentation of yellowtail founder (*Limanda ferruginea*): a live food enrichment experiment. Aquaculture 210:285–304

Cripps, G.C., Watkins, J.L., Hill, H.J. and Atkinson, A. 1999. Fatty acid content of Antarctic krill *Euphausia superba* at South Georgia related to regional populations and variations in diet. Mar. Ecol. Prog. Ser. 181:177–188

Damude, H.G. and Kinney, A.J. 2007. Engineering oilseed plants for a sustainable, land-based source of long chain polyunsaturated fatty acids. Lipids 42:179–185

Danielsdottir, M.G., Brett, M.T. and Arhonditsis, G.B. 2007. Phytoplankton food quality control of planktonic food web processes. Hydrobiologia 589:29–41

Darimont, C.T., Reimchen, T.E. and Paquet, P.C. 2003. Foraging behaviour by gray wolves on salmon streams in coastal British Columbia. Can. J. Zool. 81:349–353

Davis, B.C. and Kris-Etherton, P.M. 2003. Achieving optimal essential fatty acid status in vegetarians: current knowledge and practical implications. Am. J. Clin. Nutr. 78(Suppl):640S–646S

Dobey, S., Masters, D.V., Scheick, B.K., Clark, J.D., Pelton, M.R. and Sunquist, M.E. 2005. Ecology of Florida black bears in the Okefenokee-Osceola ecosystem. Wildlife Monogr. 158:1–41

Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J., Striegl, R.G., McDowell, W.H., Kortelainen, P., Caraco, N.F., Melack, J.M. and Middelburg, J.J. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnol. Oceanogr. 51:2388–2397

FAO. 2004. The State of World Fisheries and Aquaculture. Rome: FAO Fisheries Department

Farrell, D.J. 1998. Enrichment of hen eggs with n-3 long-chain fatty acids and evaluation of enriched eggs in humans. Am. J. Clin. Nut. 68:538–544

Fedorova, I., Hussein, N., Di Martino, C., Moriguchi, T., Hoshiba, J., Majchrzak, S. and Salem, N. Jr. 2007. An n-3 fatty acid deficient diet affects mouse spatial learning in the Barnes circular maze. Prostaglandins Leukot. Essent. Fatty Acids 77:269–277

Felicetti, L.A., Schwartz, C.C., Rye, R.O., Gunther, K.A., Crock, J.G., Haroldson, M.A., Waits, L. and Robbins, C.T. 2004. Use of naturally occurring mercury to determine the importance of cutthroat trout by Yellowstone grizzly bears. Can. J. Zool. 82:493–501

Fleurence, J., Gutbier, G., Mabeaul, S. and Leray, C. 1994. Fatty acids from 11 marine macroalgae of the French Brittany coast. J. Appl. Phycol. 6:527–532

Francis, T.B., Schindler, D.E. and Moore, J.W. 2006. Aquatic insects play a minor role in dispersing salmon-derived nutrients in southwestern Alaska. Can. J. Fish. Aquat. Sci. 63:2543–2552

Freitag, H. 2004. Composition and longitudinal patterns of aquatic insect emergence in small rivers of Palawan Island, the Philippines. Int. Rev. Hydrobiol. 89:375–391

Gardarsson, A. and Einarsson, A. 2002. The food relations of the waterbirds of Lake Myvatn, Iceland. Verh. Internat. Verein. Limnol. 28:754–763

Garg, M.L., Wood, L.G., Singh, H. and Moughan, P.J. 2006. Means of delivering recommended levels of long chain n-3 polyunsaturated fatty acids in human diets. J. Food Sci. 71:R66–R71

Geiser, F., Firth, B.T. and Seymour, R.S. 1992. Polyunsaturated dietary lipids lower the selected body temperature of a lizard. J. Comp. Physiol. B 162:1–4

Gende, S.M., Quinn, T.P. and Willson, M.F. 2001. Consumption choice by bears feeding on salmon. Oecologia. 127:372–382

Gere, G. and Andrikovics, S. 1994. Feeding of ducks and their effects on water quality. Hydrobiologia. 279/280:157–161

Gerster, H. 1998. Can adults adequately convert α-linoleic acid (18:3n–3) to eicosapentaenoic acid (20:5n–3) and docosahexaenoic acid (22:6n–3)? Int. J. Vitam. Nutr. Res. 68:159–173

Gladyshev, M.I ., Sushchik, N.N., Kalachova, G.S., Dubovskaya, O.P. and Makhutova, O.N. 2006a. Influence of sestonic elemental and essential fatty acid contents in a eutrophic reservoir in Siberia on population growth of *Daphnia* (*longispina* group). J. Plankton Res. 28:907–917

Gladyshev, M.I., Sushchik, N.N., Gubanenko, G.A., Demirchievam, S.M. and Kalachova, G.S. 2006b. Effect of way of cooking on content of essential polyunsaturated fatty acids in muscle tissue of humpback salmon (*Oncorhynchus gorbuscha*). Food Chem. 96:446–451

Gladyshev, M.I., Sushchik, N.N., Gubanenko, G.A., Demirchievam, S.M. and Kalachova, G.S. 2007. Effect of boiling and frying on the content of essential polyunsaturated fatty acids in muscle tissue of four fish species. Food Chem. 101:1694–1700

Goedkoop, W., Sonesten, L., Ahlgren, G. and Boberg, M. 2000. Fatty acids in profundal benthic invertebrates and their major food resources in Lake Erken, Sweden: seasonal variation and trophic indications. Can. J. Fish. Aquat. Sci. 57:2267–2279

Green, K.H., Wong, S.C.F. and Weiler, H.A. 2004. The effect of dietary n-3 long-chain polyunsaturated fatty acids on femur mineral density and biomarkers of bone metabolism in healthy, diabetic and dietary-restricted growing rats. Prostaglandins Leukot. Essent. Fatty Acids 71:121–130

Gulati, R.D. and DeMott, W.R. 1997. The role of food quality for zooplankton: remarks on the state-of-the-art, perspectives and priorities. Freshw. Biol. 38:753–768

Hanson, B.J., Cummins, K.W., Cargill, A.S. and Lowry, R.R. 1985. Lipid content, fatty acid composition, and the effect of diet of fats of aquatic insects. Comp. Biochem. Physiol. B 80:257–276

Harwood, J.L. 1996. Recent advances in the biosynthesis of plant fatty acids. Biochim. Biophys. Acta. 1301:7–56

Hebert, C.E., Shutt, J.L. and Ball, R.O. 2002. Plasma amino acid concentrations as an indicator of protein availability to breeding herring gulls (*Larus argentatus*). Auk 119:185–200

Hebert, C.E., Weseloh, D.V.C., Idrissi, A., Arts, M.T., O'Gorman, R., Gorman, O.T., Locke, B., Madenjian, C.P. and Roseman, E.F. 2008. Restoring piscivorous fish populations in the Laurentian Great Lakes causes seabird dietary change. Ecology 89:891–897

Heinz, E. 1993. Biosynthesis of polyunsaturated fatty acids. In: Lipid metabolism in plants. Edited by Moore, T.S. Boca Raton, USA: CRC Press, pp. 34–89

Helfield, J.M. and Naiman, R.J. 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. Ecosystems 9:167–180

Hibbeln, J.R., Nieminen, L.R.G. and Lands, W.E.M. 2004. Increasing homicide rates and linoleic acid consumption among five western countries, 1961–2000. Lipids 39:1207–1213

Hibbeln, J.R., Ferguson, T.A. and Blasbalg, T.L. 2006. Omega-3 fatty acid deficiencies in neurodevelopment, aggression and autonomic dysregulation: opportunities for intervention. Int. Rev. Psychiatry 18:107–118

Hilderbrand, G.V., Jenkins, S.G., Schwartz, C.C., Hanley, T.A. and Robbins, C.T. 1999a. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Can. J. Zool. 77:1623–1630

Hilderbrand, G.V., Hanley, T.A., Robbins, C.T. and Schwartz, C.C. 1999b. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121:546–550

Hilderbrand, G.V., Farley, S.D., Schwartz, C.C. and Robbins, C.T. 2004. Importance of salmon to wildlife: implications for integrated management. Ursus 15:1–9

Hoffman, L.C. 2008. The yield and nutritional value of meat from African ungulates, camelidae, rodents, ratites and reptiles. Meat Sci. 80:94–100

Howard, R.W. and Stanley-Samuelson, D.W. 1996. Fatty acid composition of fat body and Malpighian tubules of the tenebrionid beetle, *Zophobas atratus*: significance in eicosanoid-mediated physiology. Comp. Biochem. Physiol. B 115:429–437

Hoyer, M.V. and Canfield, D.E. Jr. 1994. Bird abundance and species richness on Florida lakes: influence of trophic status, lake morphology, and aquatic macrophytes. Hydrobiologia 297/280:107–119

Hulbert, A.J., Rana, T. and Couture, P. 2002. The acyl composition of mammalian phospholipids: an allometric analysis. Comp. Biochem. Physiol. B. 132:515–527

Huryn, A.D. and Wallace, J.B. 2000. Life history and production of stream insects. Annu. Rev. Entomol. 45:83–110

Kainz, M., Arts, M.T. and Mazumder, A. 2004. Essential fatty acids in the planktonic food web and their ecological role for higher trophic levels. Limnol. Oceanogr. 49:1784–1793

Kolanowski, W., Stolyhwo, A. and Grabowski, M. 2007. Fatty acid composition of selected fresh water gammarids (Amphipoda, Crustacea): a potentially innovative source of omega-3 LC PUFA. J. Am. Oil. Chem. Soc. 84:827–833

Koussoroplis, A.M., Lemarchand, C., Bec, A., Desvilettes, C., Amblard, C., Fournier, C., Berny, P. and Bourdier, G. 2008. From aquatic to terrestrial food webs: decrease of the docosahexaenoic acid/linoleic acid ratio. Lipids 43:461–466

Lauritzen, L., Hansen, H.S., Jorgensen, M.H. and Michaelsen, K.F. 2001. The essentiality of long chain n-3 fatty acids in relation to development and function of the brain and retina. Prog. Lipid Res. 40:1–94

Lim, S.-Y., Hoshiba, J., Moriguchi, T. and Salem, N. Jr. 2005a. N-3 fatty acid deficiency induced by a modified artificial rearing method leads to poorer performance in spatial learning tasks. Pediatr. Res. 58:741–748

Lim, S.-Y., Hoshiba, J. and Salem, N. Jr. 2005b. An extraordinary degree of structural specificity is required in neural phospholipids for optimal brain function: n-6 docosapentaenoic acid

substitution for docosahexaenoic acid leads to a loss in spatial task performance. J. Neurochem. 95:848–857

Leeper, D.A. and Taylor, B.E. 1998. Insect emergence from a South Carolina (USA) temporary wetland pond, with emphasis on the Chironomidae (Diptera). J. North Am. Benthol. Soc. 17:54–72

Leonard, A.E., Pereira, S.L., Sprecher, H. and Huang, Y.S. 2004. Elongation of long-chain fatty acids. Prog. Lipid Res. 43:36–54

MacKenzie, R.A. 2005. Spatial and temporal patterns in insect emergence from a southern Marine salt marsh. Am. Midl. Nat. 153:257–269

MacKenzie, R.A. and Kaster, J.L. 2004. Temporal and spatial patterns of insect emergence from a Lake Michigan coastal wetland. Wetlands 24:688–700

Mansour, M.P., Holdsworth, D.G., Forbes, S.E., Macleod, C.K. and Volkman, J.K. 2005. High contents of 24:6(n-3) and 20:1(n-13) fatty acids in the brittle star *Amphiura elandiformis* from Tasmanian coastal sediments. Biochem. Syst. Ecol. 33:659–674

Marion, L., Clergeau, P., Brient, L. and Bertru, G. 1994. The importance of avian-contributed nitrogen (N) and phosphorus (P) to Lake Grand-Lieu, France. Hydrobiologia 279/280:133–147

Merritt, J.F., Lima, M. and Bozinovic, F. 2001. Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. Oikos 94:505–514

Millar, J.S. and McAdam, A.G. 2001. Life on the edge: the demography of short-season populations of deer mice. Oikos 93:69–76

Mills, G.L., McArthur, J.V., Wolfe, C., Aho, J.M. and Rader, R.B. 2001. Changes in fatty acid and hydrocarbon composition of leaves during decomposition in a southeastern blackwater stream. Arch. Hydrobiol. 152:315–328

Mitchell, T.W., Ekroos, K., Blanksby, S.J., Hulbert, A.J. and Else, P.L. 2007. Differences in membrane acyl phospholipid composition between an endothermic mammal and an ectothermic reptile are not limited to any phospholipid class. J. Exp. Biol. 210:3440–3450

Musil, P. and Fuchs, R. 1994. Changes in abundance of water birds species in southern Bohemia (Czech Republic) in the last 10 years. Hydrobiologia. 279/280:511–519

Müller-Navarra, D.C. 1995. Evidence that a highly unsaturated fatty acid limits *Daphnia* growth in nature. Arch. Hydrobiol. 132:297–307

Müller-Navarra, D.C., Brett, M.T., Park, S., Chandra, S., Ballantyne, A.P., Zorita, E. and Goldman, C.R. 2004. Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes. Nature 427:69–72

Naiman, R.J., Bilby, R.E., Schindler, D.E. and Helfield, J.M. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417

Nakano, S. and Murakami, M. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proc. Natl. Acad. Sci. U.S.A. 98:166–170

Nor Aliza, A.R., Bedick, J.C., Rana, R.L., Tunaz, H., Wyatt Hoback, W. and Stanley, D.W. 2001. Arachidonic and eicosapentaenoic acids in tissues of the firefly, *Photinus pyralis* (Insecta: Coleoptera). Comp. Biochem. Physiol. A 128:251–257

Ozyurt, G. and Polat, A. 2006. Amino acid and fatty acid composition of wild sea bass (*Dicentrarchus labrax*): a seasonal differentiation. Eur. Food Res. Technol. 222:316–320

Ozyurt, G., Polat, A. and Ozkutuk, S. 2005. Seasonal changes in the fatty acids of gilthead sea bream (*Sparus aurata*) and white sea bream (*Diplodus sargus*) captured in Iskenderun Bay, eastern Mediterranean coast of Turkey. Eur. Food Res. Technol. 220:120–124

Paetzold, A., Schubert, C.J. and Tockner, K. 2005. Aquatic terrestrial linkages along a braided-river: riparian arthropods feeding on aquatic insects. Ecosystems 8:748–759

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R. and Zeller, D. 2002. Towards sustainability in world fisheries. Nature 418:689–695

Pawlosky, R.J., Denkins, Y., Ward, G. and Salem, N. Jr. 1997. Retinal and brain accretion of long-chain polyunsaturated fatty acids in developing felines: the effects of corn oil-based maternal diets. Am. J. Clin. Nutr. 65:465–472

Persson, J. and Vrede, T. 2006. Polyunsaturated fatty acids in zooplankton: variation due to taxonomy and trophic position. Freshw. Biol. 51:887–900

Plourde, M. and Cunnane, S.C. 2007. Extremely limited synthesis of long chain polyunsaturates in adults: implications for their dietary essentiality and use as supplements. Appl. Physiol. Nutr. Metabol. 32:619–634

Poepperl, R. 2000. Benthic secondary production and biomass of insects emerging from a northern German temperate stream. Freshw. Biol. 44:199–211

Polis, G.A. and Hurd, S.D. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am. Nat. 147:396–423

Politia, L., Rotsteina, N. and Carrib, N. 2001. Effects of docosahexaenoic acid on retinal development: cellular and molecular aspects. Lipids 36:927–935

Ponyi, J.E. 1994. Abundance and feeding of wintering and migrating aquatic birds in two sampling areas of Lake Balaton in 1983–1985. Hydrobiologia 279/280:63–69

Pruitt, N.L. and Lu, C. 2008. Seasonal changes in phospholipid class and class-specific fatty acid composition associated with the onset of freeze tolerance in third-instar larvae of *Eurosta solidaginis*. Physiol. Biochem. Zool. 81:226–234

Quinn, T.P., Gende, S.M., Ruggerone, G.T. and Rogers, D.E. 2003. Density-dependent predation by brown bears (*Ursus arctos*) on sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 60:553–562

Raven, J.A. and Maberly, S.C. 2004. Plant productivity of inland waters. In: Chlorophyll *a* fluorescence. Advances in photosynthesis and respiration, Vol. 19. Edited by Papageorgiou, G.C. and Govindjee. Dordrecht: Springer, pp. 779–793

Reimchen, T.E. 2000. Some ecological and evolutionary aspects of bear–salmon interactions in coastal British Columbia. Can. J. Zool. 78:448–457

Richoux, N.E., Deibel, D., Thompson, R.J. and Parrish, C.C. 2005. Seasonal and developmental variation in the fatty acid composition of *Mysis mixta* (Mysidacea) and *Acanthostepheia malmgreni* (Amphipoda) from the hyperbenthos of a cold-ocean environment (Conception Bay, Newfoundland). J. Plankton Res. 27:719–733

Robert, S.S. 2006. Production of eicosapentaenoic and docosahexaenoic acid-containing oils in transgenic land plants for human and aquaculture nutrition. Mar. Biotech. 8:103–109

SanGiovanni, J.P. and Chew, E.Y. 2005. The role of omega-3 long-chain polyunsaturated fatty acids in health and disease of the retina. Prog. Retinal Eye Res. 24:87–138

Sanzone, D.M., Meyer, J.L., Marti, E., Gardiner, E.P., Tank, J.L. and Grimm, N.B. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. Oecologia. 134:238–250

Schlechtriem, C., Arts, M.T. and Zellmer, I.D. 2006. Effect of temperature on the fatty acid composition and temporal trajectories of fatty acids in fasting *Daphnia pulex* (Crustacea, Cladocera). Lipids. 41:397–400

Shorland, F.B. 1963. The distribution of fatty acids in plant lipids. In: Chemical plant taxonomy. Edited by Swain, T. London, New York: Academic Press, pp. 253–311

Silvers, K.M. and Scott, K.M. 2002. Fish consumption and selfreported physical and mental health status. Public Health Nutr. 5:427–431

Simopoulos, A.P. 2004a. The traditional diet of Greece and cancer. Eur. J. Cancer Prevent. 13:219–230

Simopoulos, A.P. 2004b. Omega-3 fatty acids and antioxidants in edible wild plants. Biol. Res. 37:263–277

Stagliano, D.M., Benke, A.C. and Anderson, D.H. 1998. Emergence of aquatic insects from 2 habitats in a small wetland of the southeastern USA: temporal patterns of numbers and biomass. J. North Am. Benthol. Soc. 17:37–53

Stanley, D. 2006. Prostaglandins and other eicosanoids in insects: biological significance. Ann. Rev. Entomol. 51:25–44

Stanley-Samuelson, D.W., Jensen, E., Nickerson, K.W., Tiebel, K., Ogg, C.L. and Howard, R.W. 1991. Insect immune response to bacterial infection is mediated by eicosanoids. Proc. Natl. Acad. Sci. U.S.A. 88:1064–1068

Stapp, P. and Polis, G.A. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. Oecologia 134:496–504

Stapp, P. and Van Horne, B. 1997. Response of Deer Mice (*Peromyscis maniculatus*) to shrubs in shortgrass prairie: linking small-scale movements and spatial distribution of individuals. Funct. Ecol. 11:644–651

Sullivan, T.P., Lautenschlager, R.A. and Wagner, R.G. 1999. Clearcutting and burning of northern spruce-fir forests: implications for small mammal communities. J. Appl. Ecol. 36:327–344

Surh, J., Ryu, J.S. and Kwon, H. 2003. Seasonal variations of fatty acid compositions in various Korean shellfish. J. Agric. Food Chem. 51:1617–1622

Sushchik, N.N., Gladyshev, M.I., Moskvichova, A.V., Makhutova, O.N. and Kalachova, G.S. 2003. Comparison of fatty acid composition in major lipid classes of the dominant benthic invertebrates of the Yenisei River. Comp. Biochem. Physiol. B 134:111–122

Sushchik, N.N., Gladyshev, M.I., Makhutova, O.N., Kalachova, G.S., Kravchuk, E.S. and Ivanova, E.A. 2004. Associating particulate essential fatty acids of the ω3 family with phytoplankton species composition in a Siberian reservoir. Freshw. Biol. 49:1206–1219

Sushchik, N.N., Gladyshev, M.I., Kalachova, G.S., Makhutova, O.N. and Ageev, A.V. 2006. Comparison of seasonal dynamics of the essential PUFA contents in benthic invertebrates and grayling *Thymallus arcticus* in the Yenisei River. Comp. Biochem. Physiol. B. 145:278–287

Sushchik, N.N., Gladyshev, M.I. and Kalachova, G.S. 2007. Seasonal dynamics of fatty acid content of a common food fish from the Yenisei River, Siberian grayling, *Thymallus arcticus*. Food Chem. 104:1353–1358

Suter, W. 1994. Overwintering waterfowl on Swiss lakes: how are abundance and species richness influenced by trophic status and lake morphology? Hydrobiologia 279/280:1–14

Szepanski, M.M., Ben-David, M. and Van Ballenberghe, V. 1999. Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. Oecologia 120:327–335

Tocher, D.R., Leaver, M.J. and Hodson, P.A. 1998. Recent advances in the biochemistry and molecular biology of fatty acyl desaturases. Prog. Lipid Res. 37:73–117

Uscian, J.M. and Stanley-Samuelson, D.W. 1994. Fatty acid compositions of phospholipids and triacylglycerols from selected terrestrial arthropods. Comp. Biochem. Physiol. B 107:371–379

Vanni, M.J., Layne, C.D. and Arnott, S.E. 1997. "Top-down" trophic interactions in lakes: effects of fish on nutrient dynamics. Ecology 78:1–20

Wetzel, R.G. 1992. Gradient-dominated ecosystems: sources and regulatory function of dissolved organic matter in freshwater ecosystems. Hydrobiologia 229:181–198

Willson, M.F., Gende, S.M. and Marston, B.H. 1998. Fishes and the forest. BioScience. 48:455–462

Winder, M., Schindler, D.E., Moore, J.W., Johnson, S.P. and Palen, W.J. 2005. Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? Can. J. Fish. Aquat. Sci. 62:2285–2293

Wolff, R.L., Lavialle, O., Pëdrono, F., Pasquier, E., Deluc, L.G., Marpeau, A.M. and Aitzetmüller, K. 2001. Fatty acid composition of Pinaceae as taxonomic markers. Lipids 36:439–451

Wood, J.D., Enser, M., Fisher, A.V., Nute, G.R., Sheard, P.R., Richardson, R.I., Hughes, S.I. and Whittington, F.M. 2008. Fat deposition, fatty acid composition and meat quality: a review. Meat Sci. 78:343–358

Woollhead, J. 1994. Birds in the trophic web of Lake Esrom, Denmark. Hydrobiologia. 279/280:29–38

Zenebe, T., Ahlgren, G. and Boberg, M. 1998. Fatty acid content of some freshwater fish of commercial importance from tropical lakes in the Ethiopian Rift Valley. J. Fish Biol. 53:987–1005