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Effect of temperature and tissue type on fatty acid signatures of two species of North Pacific juvenile gadids: A laboratory feeding study

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ABSTRACT

The utility of the fatty acid biomarker (FAB) approach in fisheries ecology is limited by our understanding of how biotic and abiotic factors determine dietary markers in fish tissues. An 8-week laboratory experiment was conducted on two species of juvenile gadids (Pacific cod, *Gadus macrocephalus* and walleye Pollock, *Theragra chalcogramma*) reared at 3 °C or 9 °C and fed a diet enriched with either oils of marine origin or terrestrial plant origin. Non-linear models were fitted to investigate how tissue type and temperature mediated the proportion of FABs in fish. Across temperatures, fatty acid (FA) profiles were similar for both species of gadids. FAs also showed high temporal sensitivity across temperatures, and were evident in fish after only one week of feeding. Pacific cod held at 9 °C and fed a terrestrial plant oil (TPO) enriched diet had significantly higher C_{18} polyunsaturated FAs (PUFAs) in their liver than cod held at 3 °C after one week, but this temperature effect diminished as tissues reached equilibrium with their diet. C_{18} PUFAs were significantly higher in liver than in muscle. Differential proportions of C_{18} PUFAs among tissues provide temporal patterns that may help with disentangling the timing of offshore–inshore nursery migrations in juvenile fish. Calibration coefficients were determined to explain the relationship between FAs in the diet and FAs in fish tissues. These coefficients will support future development of quantitative estimates of diet in juvenile low-fat fish.

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1. Introduction

For decades scientists have been searching for rules to explain observed patterns of energy flow in food webs (Elton, 1927), reflecting the importance of predator–prey relationships in explaining patterns of community organization (Paine, 1980). There are a number of constraints to accurately determine predator–prey relationships in juvenile fish via traditional gut analyses (Cortes, 1997; Vander Zanden et al., 1997). Briefly, these include underrepresentation of small and/or soft prey items and missing diet data beyond the most recent meal. Therefore, trophic ecologists now use biomarker methods (e.g., lipid classes, fatty acids, bulk stable isotope and compound specific isotopes) to resolve food web linkages (Canuel et al., 1997; Jaschinski et al., 2008; Kharlamenko et al., 2001).

In the last three decades, fatty acid biomarkers (FABs) have been used to define food web relationships in both marine (Dalsgaard et al., 2003; Sargent, 1976) and freshwater ecosystems (Arts and Wainman, 1999). The FAB approach is based on the distinctive FA signatures of primary producers (Budge et al., 2006; Iverson, 2009) which are integrated conservatively into secondary consumers such as zooplankton (Sargent, 1989; Sargent et al., 1987; Stevens et al., 2004). In fish, FABs have been used qualitatively to identify both dietary and habitat shifts in larval and juvenile stages (St. John and Lund, 1996). However, most studies on juvenile fish have used a qualitative approach to FAB analysis, with few quantitative examples of diet estimation (Budge et al., 2012; Dalsgaard and St. John, 2004).

Quantitative fatty acid signature analysis (QFASA), the use of unique prey species FA signatures to assign quantitative estimates of predator diet, is now being applied to higher trophic levels such as marine mammals (Beck et al., 2007), sea birds (Iverson et al., 2007) and polar bears (Thiemann et al., 2008). A prerequisite to the QFASA approach is controlled laboratory studies in which predators are fed one prey diet until

Abbreviations: (ANOVA), analyses of variance; (BAME), Bacterial Fatty Acid Methyl Ester; (CC), calibration coefficients; (FAs), fatty acids; (FABs), fatty acid biomarkers; (FAME), FA methyl esters; (GLM), generalized linear model; (HMSC), Hatfield Marine Science Center; (MO), marine oil; (MUFAs), monounsaturated fatty acids; (PL), phospholipids; (PUFAs), polyunsaturated fatty acids; (QFASA), quantitative fatty acid signature analysis; (SFAs), saturated fatty acids; (SGR), specific growth rate; (TPO), terrestrial plant oil; (TLC/FID), thin layer chromatography/flame ionization detection; (TAG), triacylglycerols; (WWT), wet weight.

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the predator tissue resembles the prey as closely as possible (Budge et al., 2011, 2012; Wang et al., 2010). This results in a "calibration coefficient" for each FA which takes into account predator metabolism and is the ratio of the FA in the predator relative to the proportion in its diet. However, significant knowledge gaps in how fish modify prey fatty acids through elongation and desaturation still prevent the quantitative application of the FAB approach (Budge et al., 2011, 2012). In addition, little is known about how FA metabolism in fish is affected by a range of abiotic and biotic factors that determine growth (temperature, ration, species-specific physiology, prey type and ontogeny). Proportions of FAs measured in fish may be further mediated by growth independent effects such as tissue type and condition, resulting in interactions between growth and these factors.

In the Northeast Pacific semi-pelagic walleye pollock (*Theragra chalcogramma*) and demersal Pacific cod (*Gadus macrocephalus*) are the two most commercially important species in the Alaskan finfish fishery. Both species have pelagic larvae (4–30 mm) that settle at ~45 mm into complex biogenic habitat (eelgrass, kelp) in shallow, coastal areas (2–4 m; Laurel et al., 2007). These nursery areas can be within meters of shore and are prone to terrestrial run-off through annual late-spring freshets when juvenile gadids begin to settle. Short chain C_{18} PUFAs (18:2n − 6 and 18:3n − 3) are not unique to terrestrial material and are also found in high levels in green algae and eelgrass blades (Brett et al., 2009; Copeman et al., 2009). However, previous studies on cold water marine systems using both FABs and compound specific isotopes of FAs have shown that elevated proportions (>4%) of these two FAs in marine systems are indicative of nearshore dietary carbon input, often of terrestrial origin (Budge et al., 2001; Copeman et al., 2009; Ramos et al., 2003). Controlled laboratory studies looking at the retention of dietary nearshore FA indicators may help indicate residency times, a key component of understanding habitat connectivity and nursery function for coastal gadids.

We conducted a laboratory study to examine the proportions of 18:3n − 3 and 18:2n − 6 in the muscle and liver of two species of juvenile gadids. The level of FAs in fish fed two different gel food diets was measured in relation to species and culture temperature during an 8-week feeding trial. Diets were identical, except that one was enriched with marine oil (MO, cod liver) while the other was enriched with terrestrial plant oil (TPO, flax seed). Over our 8-week study we specifically examined the degree to which tissue proportions of C_{18} PUFAs were: 1) species-specific, 2) mediated by culture temperature, 3) specific to tissue type (liver, muscle) and 4) vary temporally between tissue types (i.e. FAB in liver:FAB in muscle). A further objective of our study was to provide the first calibration coefficients for low fat juvenile marine fish. These coefficients for both liver and muscle tissues could be used to develop quantitative approaches to diet determination in cold-water marine fish.

2. Materials and methods

2.1. Fish husbandry and sampling

Juvenile walleye pollock were collected in early June 2008 with lights and lift nets suspended from a dock in Pt. Townsend Bay, Washington, USA (48°6′N 122°48′W). Fish were held for 24 h in ambient seawater prior to shipment to the National Marine Fisheries Service laboratory at Hatfield Marine Science Center (HMSC) in Newport, Oregon, USA. At HMSC, pollock (20–40 mm initial total length) were fed a mixture of krill (*Euphausia superb*) and gel food (Table 1) to satiation 3 times per week. Pollock were held in flow-through seawater tanks (3140 L) at 9 °C until the start of the experiment in October.

Pacific cod were collected in Kodiak, Alaska (USA) by beach seine in mid July 2008 and were allowed to depurate for 24 h prior to overnight shipment in containers with an overlying saturated O_2 layer. On arrival at HMSC, cod (20–50 mm initial total length) were held in 3104 L tanks

Table 1
Ingredients in maintenance gel-food (herring), MO enriched gel-food (Pacific cod fillets and cod liver oil) and TPO enriched gel-food (Pacific cod fillets and flax seed oil) diets.

Ingredient	Maintenance diet[a] (g/kg)	MO diet (g/kg)	TPO diet (g/kg)
Herring	139.5	0.0	0.0
Pacific cod	0.0	138.0	138.0
Cod liver oil	0.0	11.1	0.0
Flaxseed oil	0.0	0.0	11.1
Freeze dried krill	7.0	6.9	6.9
Squid	69.8	69.0	69.0
Otohime EP4[b]	212.2	209.9	209.9
TwinLab Amino Fuel[c]	16.2	16.0	16.0
Powdered gelatin[d]	137.1	135.6	135.6
Water	417.6	413.0	413.0
Vitamins[e]	0.6	0.6	0.6

Contained: pro vitamin A, vitamin A, vitamin C, vitamin D, vitamin E, thiamin, riboflavin, niacin, vitamin B-6, folic acid, vitamin B12, biotin, pantothenic acid, calcium, iron, iodine, magnesium, zinc, selenium, copper, manganese, chromium, molybdenum, choline, inositol and floraglo lutein.

[a] Fed for >6 weeks prior to onset of feeding experiment.

[b] Otohime EP4, extruded pellet manufactured by: Marubeni Nisshin Feed Co., Ltd., Tokyo, Japan and imported by: Reed Mariculture Inc., Campbell, CA 95008, USA. Feed contains: krill meal, fish meal, squid meal, wheat flour, potato starch, corn starch, fish oil, calcium phosphate, betaine, soy lecithin, licorice plant and wheat germ.

[c] Amino Fuel, Ideasphear Inc., American Fork, UT, USA.

[d] Knox unflavored Gelatine, Krafts Foods Global Inc., Northfield, IL, USA.

[e] TwinLab Daily One Caps with Iron, Ideasphere Inc., American Fork, UT, USA.

at 9 °C on the same feeding schedule as pollock until the beginning of the feeding trial in early October.

Prior to the experiment, 25 randomly selected walleye pollock and 25 Pacific cod were measured to assess their initial size at the beginning of the experiment: total length of 61.6 ± 4.3 mm and 61.8 ± 3.7 mm, respectively. Five days prior to the experiment, tanks were randomly stocked with either 12 juvenile pollock per tank or 10 juvenile cod. Dietary trials were run in twenty-four cylindrical upwelling 100 L tanks with water flow-through at 1.5 $L \cdot min^{-1}$. Twelve of the tanks were gradually lowered to 3 °C over a 3-day period (2°/day) while the other tanks remained at 9 °C. The 24 experimental tanks consisted of 3 tanks for each species (cod or pollock) at each temperature (9 °C or 3 °C) replicated for two different dietary treatments (MO or TPO enriched gel food).

The feeding trial started October 7, 2008 and fish were hand-fed enriched gel-food diets to satiation 5× weekly. Diets were formulated to contain the same level of lipid per wet weight and the same lipid class composition (Tables 1 & 2). Gelatinized diets, previously shown to provide adequate nutrition for Pacific marine juveniles gadids (Hurst et al., 2010), were modified by addition of either marine oil (MO, cod liver oil) or terrestrial plant oil (TPO, flax seed oil). Diets contained a combination of squid, krill, Pacific cod fillets, commercial food, amino acid supplements, and vitamins (Table 1). Ingredients were blended together and then bound by addition of a warm gelatin. Diets were frozen immediately after addition of the gelatin. Small (~1 cm wide) strands of gel food, suitable for juvenile fish gape size, were produced by grating frozen blocks of gel food using a cheese grater.

Three pollock and three cod were sampled for lipid analyses at the beginning of the experiment (time-0) prior to the introduction of diet treatments. Fish were first euthanized and then blotted dry with paper towels and total length (mm) and wet weight (g) were recorded. During tissue sampling, liver and white muscle were sampled separately from each animal. White muscle (0.25–0.35 g wet weight) was collected from each fish along the dorsal margin, by first dissecting the skin and then sampling halfway along the anterior–posterior plane. Whole liver samples (0.02 to 0.20 g) were also collected by dissection on ice. Lipid sampling was conducted on three fish per species at time zero and on one fish per tank at the end of weeks 1, 2, 4 and 8 giving a total of 3 samples of liver and 3 samples of muscle per treatment at four time periods.

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