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Benthic enrichment by diatom-sourced lipid promotes growth and condition in juvenile Tanner crabs around Kodiak Island, Alaska

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ABSTRACT: Nearshore embayments are important nurseries for juvenile southern Tanner crabs *Chionoecetes bairdi*, as they provide refuge from predation and elevated water temperatures promote rapid growth. Previous investigations of juvenile Tanner crabs have shown considerable variability in size of age-0 yr crabs from different shallow water embayments surrounding Kodiak, Alaska. To determine the proportion of this presumed growth variability that is due to diet quality, we sampled crabs and sediments over 2 yr at nursery sites that had previously demonstrated disparate age-0 yr crab sizes. Juvenile crabs reside at the sediment–water interface and therefore we measured sedimentary grain size and sedimentary organic matter, as well as total lipids per weight, lipid classes and fatty acid biomarkers in both crabs and sediments. Juvenile crabs from sheltered sites, as opposed to exposed sites, were characterized by larger size and by rapid growth rates and higher tissue lipid densities. Further, higher diatom and bacterial fatty acid markers characterized both sedimentary lipids and crab lipids in animals from sheltered bays compared to those from exposed sites. Controlled laboratory experiments were run to determine the relative importance of food quantity (ration) and quality (% lipid) on juvenile growth and condition. We found both diet quantity and quality significantly affected growth and lipid storage of juvenile crabs. Our results point to the importance of trophic factors in defining high quality habitat for a commercially important cold-water crab species.

KEY WORDS: Juvenile Tanner crab · Lipids · Fatty acids · Nursery · Food quality

INTRODUCTION

Stocks of North Pacific crab species have declined precipitously during the last 3 decades. Affected species include red king crab *Paralithodes camtschaticus*, blue king crab *P. platypus*, snow crab *Chionoecetes opilio* and southern Tanner crab *C. bairdi*. The reasons for these declines are poorly understood, but have generally been attributed to over-fishing and/or climatic changes (Armstrong et al. 1998, Woodby et al. 2005). While existing surveys are adequately monitoring sub-adult and adult populations, a more holistic understanding of the mechanisms that have forestalled recovery is hampered by incomplete information on the early life-history of *Paralithodes* and *Chionoecetes* species. First, because smaller juveniles are not sampled by large survey trawls or standard pots, there is little information on which habitats

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juveniles rely on during their first several years. Second, precise aging methods do not exist, and there is little information on growth rates in early juveniles and how growth and survival is influenced by physical and biotic parameters such as temperature and habitat quality.

While recent interest in stock enhancement has led to a rapid expansion in knowledge regarding juvenile life-history for *Paralithodes* species (Stoner et al. 2010, 2013, Daly & Long 2014), much less is known about *Chionoecetes* species. In general, juvenile *Chionoecetes* species tend to occupy sedimentary bottoms (Rosenkranz et al. 1998), unlike the *Paralithodes* crabs that utilized rugose bottoms with associated attached plants and animals (Palacios et al. 1985, Stevens & Lovrich 2014). Of the 2 commercially exploited *Chionoecetes* species, the snow crab is an Arctic species that occupies relatively deep and cold waters in the Arctic, North Pacific and North Atlantic. In contrast, the southern Tanner crab is a sub-Arctic species with populations in the North Pacific extending from the southern Bering Sea and Aleutian Islands, southward through the Gulf of Alaska to Puget Sound (Fong & Dunham 2007, Ryer et al. 2016). In the Gulf of Alaska, Tanner crabs settle from April through June and reach the C3 to C6 juvenile crab molt stages by the end of August (Ryer et al. 2015).

Deviations from a 'nominal' growth schedule may result from local environmental conditions, particularly in the early juvenile stages. As is typical of ectotherms (Hartnoll 2001), growth in North Pacific crabs is highly temperature dependent (Stevens 1990, Stoner et al. 2010, 2013, Ryer et al. 2016). We have observed differences in sizes of recently recruited age-0 yr Tanner crabs at 4 study sites around Kodiak Island, Alaska (Ryer et al. 2015), over 2 consecutive years. At 2 of these sites, Womens Bay and Kalsin Bay, crabs are larger by July and August than at the other 2 sites, Holiday Beach and Pillar Creek Cove (see Fig. 1). While the sites do not differ appreciably in spring/summer temperatures (Ryer et al. 2015), they do differ in exposure to wave action from the Gulf of Alaska. Both Holiday Beach and Pillar Creek Cove are exposed to strong wave action, whereas Womens Bay and Kalsin Bay have less wave exposure. Observations of the seafloor at these sites by divers as well as a video camera sled indicate that sediments are generally finer at Womens and Kalsin than at Holiday and Pillar (authors' pers. obs.).

We suspect that the observed difference in juvenile Tanner crab growth between sites may be explained by differences in available food resources, as defined by both the quantity and quality of prey items. Generally, the nutritional quality and quantity of organic matter associated with sediments is inversely correlated with sediment grain size (Longbottom 1970, Hargrave 1972, Cammen 1982). In turn, higher organic content supports a more diverse meiofaunal and macrofaunal community (Cammen 1982). We have observed age-0 yr Tanner crabs in seawater tanks consuming not only macrofauna such as polychaetes, but also detrital material (C. Ryer pers. obs.). Just as lower wave action and currents allow for the accumulation of finer sediments, this should also allow for the accumulation of labile organic materials (Zimmerman & Canuel 2001). At protected sites around Kodiak, we have observed the accumulation of a surficial 'fluff' during the late spring and early summer, which we presume to be composed of phytoplankton.

In seasonally cold boreal and Arctic environments, the flux of spring phytoplankton blooms to the benthos represents an essential source of nutrition for juvenile invertebrates (Budge & Parrish 1998, Parrish 1998, Richoux et al. 2004). Both high sediment respiration rates and invertebrate benthic biomass have been reported in cold-water regions that show a high carbon deposition rate to the benthos and elevated sediment organic carbon content following the spring bloom (Grebmeier 1993, Grebmeier et al. 2015). Lipids in particular are one of the important macronutrients that flux to the benthos and are important to newly settled invertebrates, as they are carbon rich and an important metabolic fuel (Copeman & Parrish 2003, Parrish et al. 2005). Further, fluxing phytoplankton lipid pools contain high proportions of phospholipids that are rich in polyunsaturated fatty acids (PUFAs) that are essential to juvenile stages of many different invertebrate species (Richoux et al. 2005, Kelly & Scheibling 2012). The analysis of fatty acid (FA) pools in marine organisms has become increasingly common in ecological studies as FAs can provide time-integrated information about trophic relationships (Dalsgaard et al. 2003, Budge et al. 2006, Parrish 2013). FA biomarkers are often produced at lower trophic levels and can correlate with various sources of primary production such as bacteria, diatoms and terrestrial runoff (Budge & Parrish 1998, Dalsgaard et al. 2003, Copeman et al. 2009). FA biomarkers are, to a degree, conservatively transferred from lower to higher trophic levels and have been previously utilized to indicate dietary sources in both invertebrates (Spilmont et al. 2009, Kelly & Scheibling 2012, Galloway et al. 2014) and fish (St John & Lund 1996, Copeman et al. 2016).

Studies on cold-water crab nutrition have demonstrated increased molt success, lipid storage, survival

and growth in larval and glaucothoe stages of cold-water Alaskan crabs in response to diets enriched with high proportions of PUFAs or live-feeds enriched with diatom lipids (Stevens et al. 2008, Beder 2015). Therefore, we hypothesized that the differences in age-0 yr Tanner crab growth at our Kodiak nursery sites is attributable to physical process that regulate the flux and accumulation of labile organic materials, thus controlling habitat trophic quality for benthic fauna, including juvenile Tanner crabs.

To evaluate this hypothesis, we compared not only the size of crabs at selected sites, but their condition, as measured by gravimetric indicators and total body lipid content. Further, we quantified the contribution of specific FAs in crabs to provide insight into the source of dietary organic matter. Next, we measured sediment grain size, total organic content, total lipids and FA profiles in sediments at selected sites to determine whether high-growth sites receive a greater input of water column productivity. Lastly, we conducted a laboratory experiment to assess the role food quantity and quality (i.e. lipid content) play in mediating the growth and lipid storage of juvenile Tanner crabs.

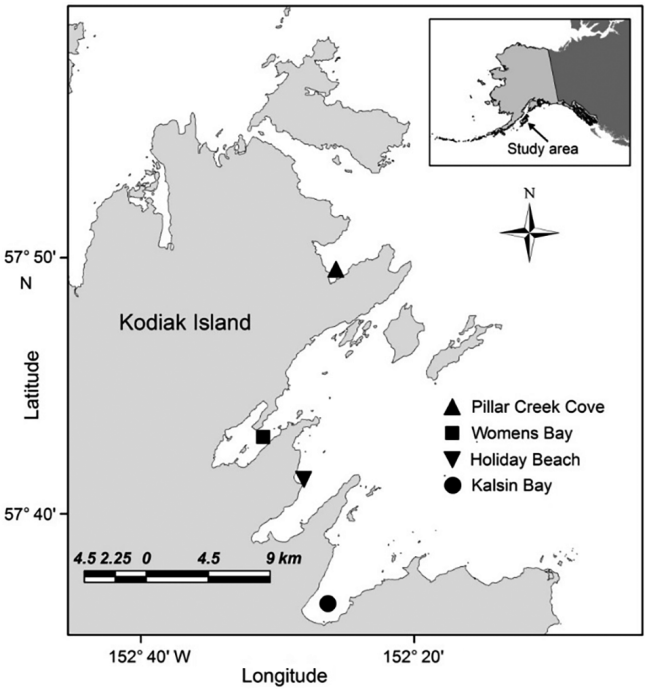

Fig. 1. Location of the juvenile Tanner crab field study sites located on Kodiak Island, Alaska, USA. Study sites include Pillar Creek Cove, Womens Bay, Holiday Beach and Kalsin Bay shown with Alaska (inset)

MATERIALS AND METHODS

Study sites

Four sites (Fig. 1) in the coastal waters of Kodiak, Alaska, were studied, all of which have been the subject of prior Tanner crab research (Ryer et al. 2015). The first 2 sites, Holiday Beach (hereafter Holiday; 57° 41.344′ N, 152° 27.958′ W) and Pillar Creek Cove (hereafter Pillar; 57° 49.136′ N, 152° 25.314′ W), have gently sloping sandy bottoms off beaches exposed to wave action from the Gulf of Alaska. The third site, in Kalsin Bay (hereafter Kalsin; 57° 36.207′ N, 152° 26.890′ W) also has a gently sloping bottom but is more protected by virtue of its location at the head of the bay, and has finer sediments characterized by silty sands. The fourth site, Womens Bay (hereafter Womens; 57° 42.800′ N, 152° 31.134′ W) has offshore islands and a narrow entrance with a shallow sill, features which protect the inner bay from wave action. Also with a gently sloping bottom, Womens has the finest sediments of the 4 sites, characterized by silty mud. Spring/summer salinity and water temperature are generally comparable between sites, ranging from 28 to 32 psu and 5 to 11°C, respectively, for all 4 sites (Ryer et al. 2015)

Crab collection

Details of crab collection protocols can be found in Ryer et al. (2015). Briefly, crabs were collected using an epi-benthic sled at each site during July and August 2010, 2011 and 2012. The codend of the sled was made of 3 mm mesh seine fabric, which retained C2 (molt stage 2) and larger juvenile Tanner crabs. The sled was towed along the seafloor at depths of 10 to 30 m, parallel to shore, at a speed of 0.5 m s^{-1} for ~30 m. GPS waypoints at the beginning and end of tows allowed for calculation of area swept. To compare end-of-summer crab size between sites, 1970 representative crabs from across the range of sampled depths from August collections at each site and year combination were measured. The number of crabs measured for site and year combinations ranged from 63 (Pillar in 2011) to 307 (Kalsin in 2012). Carapace width (CW) was measured using digital calipers, to the nearest 0.01 mm. Variance and normality issues with carapace width data precluded a holistic analysis of variance (ANOVA) approach, so we conducted individual nonparametric Kruskal-Wallis ANOVAs (Sokal & Rohlf 1969) to compare carapace width between study sites for each year.

Condition metrics based on CW–weight relationships were performed on additional crabs collected in 2010 and 2012. Selected crabs from our most disparate study sites, Pillar and Womens, were individually frozen in the field and shipped at −20°C overnight to the Hatfield Marine Science Center in Newport Oregon, where they were stored at −80°C for <6 mo before processing. Intact crabs (n = 174) without missing limbs from dominant molt stages during 2012 (C3: Pillar n = 29, Womens n = 42; C4: Pillar n = 40, Womens n = 63), were thawed and measured for CW (nearest 0.001 mm). Crabs were then rinsed with 3% ammonium formate solution to remove excess salt, then gently blotted dry and transferred to pre-weighed 43 mm aluminum foil weight boats. After initial weighing, crabs were dried at 70°C for 48 h. Foils with crabs were reweighed, then burned in a muffle furnace for 12 h at 450°C, then re-weighed again. Crab weights were calculated by subtracting the weight of the pre-weighed foils from the first 2 weights (dry weight [DWT] and wet weight [WWT], respectively), while ash free dry weights (AFDW; i.e. organic weights) were calculated by subtracting the ash weight from the previously calculated DWTs. We calculated 2 condition metrics: (1) a size standardized condition index based on the log(DWT) divided by CW and (2) the relative organic material or % AFDWT (100(AFDWT/DWT)). So as to model the relationship between body mass and CW, log-transformed WWTs, DWTs, and AFDWTs were regressed against CW (Sokal & Rohlf 1969). The distributions of weight data (WWTs, DWTs, AFDWTs) were distinctly discontinuous, given the disparities in size between C3 and C4 crabs. Accordingly, to examine differences in weights between Pillar and Womens, we conducted separate analyses for each molt stage (C3 and C4). Where raw or log-transformed weight data were normally distributed, the 2-sample *t*-test (Sokal & Rohlf 1969) was utilized, otherwise the Wilcoxon rank sum tests was utilized.

Another 146 of the crabs from Womens and Pillar were selected for total lipid analysis. These crabs came from collection depths of 10 to 30 m and represented the dominant molt stages at Pillar and Womens during July and August 2010 (Pillar C4 n = 36, Women C4 n = 10) and 2012 (Pillar C3 n = 20, Women C3 n = 20, Pillar C4 = 20, Women C4 = 40). Crabs were quickly processed over ice for CW and WWT, as described above, and then whole crabs were stored in 2 ml of ice-cold chloroform under a layer of nitrogen gas and placed in a −20°C freezer for later lipid extraction (within 1 mo). Of these, 100 crabs from 2012 (Pillar: 40, Womens: 60) were also analyzed for proportional contribution of specific FAs, to provide a comparison with FA composition of sediment at Pillar and Holiday. Procedures for lipid class and FA analysis are described below.

Sediment collection and analysis

During August 2012, sediment samples for grain size and organic content analysis were taken with a 0.1 m^2 van Veen grab, at depths ranging from 5 to 25 m, at 5 m increments, although not all depths were sampled at each site. A total of 50 grabs were taken. A plastic spoon was used to scoop 10 to 20 cm^3 of surface sediment (<3 cm depth) from each core into individual plastic bags, which were placed on ice and later frozen. In the laboratory, each sediment sample was processed to determine percent silt–clay fraction and organic content by weight. Approximately 50 g of thawed sediment was dried for 72 h at 50°C in pre-weighed aluminum pans, weighed, then burned at 550°C for 4 h and reweighed to determine percentage organic content. Another subsample of sediment was washed through a 0.062 mm mesh sieve to separate the silt–clay and sand fractions. Both the filtrate and the sediment retained by the sieve were similarly placed in pre-weighed aluminum pans, dried at 50°C for 72 h and then re-weighed to determine the percent silt–clay fraction by weight. We pooled depths and statistically compared both the % silt–clay fraction and % organic content between sites using Kruskal-Wallis non-parametric ANOVA.

Sediment samples for FA profile analysis were also taken during August 2012 at Pillar and Womens, by divers using 13 cm inner diameter acrylic core tubes. A total of 12 cores were taken at each site, at depths of 15 to 20 m (Table 1). The tube was inserted into the bottom and then the open end of the tube was plugged with a rubber stopper. The tube was then carefully removed from the bottom. While maintaining the core vertically, and with one hand under the core tube so as to prevent loss of sediment, the intact core was brought to the surface and passed to the support vessel. Onboard, the core was placed on a table and the rubber stopper removed. A piece of flexible tubing was used to siphon the fluff material into a sample jar. We use the term 'fluff' for the flocculent mixture of organic and inorganic material that rested on the sediment surface. Next, the remaining water was siphoned from the core tube and a plastic spoon was used to scoop 10 to 20 cm^3 of surface sediment (<3 cm depth). Sediment samples (n = 24) were placed in plastic bags, and along with fluff sam-

Table 1. Detailed lipid class and fatty acid composition of Tanner crabs and cores collected in July and August of 2012 from Womens and Pillar nursery habitats. Data for crabs and cores averaged across depth. A total of 48 sediment samples were analyzed for lipid and fatty acid parameters, 146 crabs were analyzed for total lipids and lipid classes and 100 crabs were analyzed for fatty acids. Data are means ± SE

	Womens crabs		Womens cores		Pillar crabs		Pillar cores	
	C3	C4	Sediment	Fluff	C3	C4	Sediment	Fluff
Number of samples	20	50	12	12	20	56	12	12
Hydrocarbons	0.1 ± 0.0	0.1 ± 0.0	6.5 ± 1.3	7.0 ± 1.0	0.2 ± 0.0	0.1 ± 0.0	7.8 ± 1.2	5.7 ± 1.3
Triacylglycerols	27.5 ± 2.0	24.3 ± 2.0	4.6 ± 1.8	6.2 ± 3.4	3.8 ± 1.1	7.6 ± 1.8	18.7 ± 3.0	9.3 ± 2.1
Sterols	11.0 ± 0.4	12.2 ±0.5	3.6 ± 1.3	8.6 ± 2.8	16.2 ± 0.7	17.5 ± 0.9	8.0 ± 3.0	11.2 ± 2.8
Acetone mobile polar lipids	0.7 ± 0.1	0.4 ± 0.0	24.4 ± 2.2	20.9 ± 1.8	0.7 ± 0.1	0.3 ± 0.0	17.5 ± 2.9	21.8 ± 2.6
Phospholipids	47.8 ± 1.4	50.9 ± 1.3	38.6 ± 3.2	35.9 ± 1.6	56.9 ± 2.4	60.5 ± 1.3	24.8 ± 3.4	18.2 ± 3.3
Number of samples	20	20	12	12	20	40	12	12
14:0	1.6 ± 0.1	1.6 ± 0.1	7.1 ± 0.3	4.4 ± 0.1	0.8 ± 0.1	1.0 ± 0.1	5.7 ± 0.5	4.1 ± 0.2
16:0	14.0 ± 0.2	13.9 ± 0.2	16.3 ± 0.8	10.6 ± 0.5	14.1 ± 0.2	13.6 ± 0.1	20.2 ± 0.7	13.2 ± 0.3
18:0	4.0 ± 0.1	4.0 ± 0.1	3.7 ± 0.7	2.5 ± 0.1	4.7 ± 0.1	4.7 ± 0.1	3.9 ± 0.8	1.6 ± 0.1
∑SFA	**21.5 ± 0.2**	**21.4 ± 0.2**	**36.9 ± 1.4**	**27.4 ± 0.8**	**21.4 ± 0.3**	**21.0 ± 0.2**	**35.8 ± 0.6**	**26.0 ± 0.4**
16:1n-7	5.8 ± 0.4	5.1 ± 0.3	29.3 ± 1.1	28.7 ± 0.8	2.8 ± 0.2	3.3 ± 0.2	31.9 ± 2.3	28.3 ± 0.7
18:1n-9	7.3 ± 0.2	7.4 ± 0.2	2.7 ± 0.2	1.7 ± 0.1	6.8 ± 0.1	6.4 ± 0.1	5.4 ± 0.4	2.2 ± 0.2
18:1n-7	6.0 ± 0.1	6.0 ± 0.1	6.1 ± 0.3	6.7 ± 0.4	7.3 ± 0.2	7.9 ± 0.1	3.8 ± 0.3	4.5 ± 0.2
20:1n-11	1.4 ± 0.1	1.3 ± 0.1	–	–	0.6 ± 0.1	0.8 ± 0.1	–	–
∑MUFA	**27.1 ± 0.4**	**26.1 ± 0.4**	**42.8 ± 1.1**	**41.3 ± 1.0**	**23.2 ± 1.0**	**23.7 ± 0.4**	**43.7 ± 2.2**	**38.0 ± 0.6**
20:4n-6	3.1 ± 0.1	3.0 ± 0.1	0.9 ± 0.1	2.4 ± 0.3	2.4 ± 0.1	2.7 ± 0.1	0.6 ± 0.1	2.2 ± 0.1
20:5n-3	23.1 ± 0.4	24.1 ± 0.4	7.1 ± 0.9	10.5 ± 1.0	27.3 ± 0.5	26.7 ± 0.3	5.0 ± 0.6	14.5 ± 0.5
22:5n-3	2.1 ± 0.12	2.1 ± 0.1	0.0 ± 0.0	0.2 ± 0.2	1.9 ± 0.1	3.2 ± 0.2	0.0 ± 0.3	0.3 ± 0.2
22:6n-3	13.8 ± 0.5	14.3 ± 0.3	1.2 ± 0.2	1.6 ± 0.2	15.5 ± 0.9	14.8 ± 0.3	0.6 ± 0.2	1.5 ± 0.1
∑PUFA	**49.9 ± 0.5**	**51.0 ± 0.5**	**20.3 ± 1.8**	**31.3 ± 1.6**	**53.9 ± 1.1**	**53.5 ± 0.5**	**17.3 ± 1.5**	**36.0 ± 0.6**
Bacterial (∑odd and branched)	4.1 ± 0.1	4.0 ± 0.1	14.9 ± 0.6	15.7 ± 0.7	2.7 ± 0.1	3.0 ± 0.2	9.3 ± 0.7	10.7 ± 0.3
Diatom (16:1n-7/16:0)	0.4 ± 0.0	0.4 ± 0.0	1.9 ± 0.1	2.8 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	1.6 ± 0.1	2.2 ± 0.1
Nearshore indicators								
∑18:2n-6 +18:3n-3	1.0 ± 0.0	1.2 ± 0.1	1.3 ± 0.0	1.7 ± 0.1	0.9 ± 0.0	0.9 ± 0.0	1.4 ± 0.1	2.3 ± 0.2
Terrestrial ∑22:0 +24:0	0.2 ± 0.0	0.2 ± 0.0	0.6 ± 0.2	0.6 ±0.2	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.7 ± 0.1

ples (n = 24), placed in a cooler with ice and returned to the lab within 6 h, where they were frozen (–20°C) for later FA profile analysis (see below).

Laboratory growth experiments

Two laboratory growth experiments were conducted. The first examined the influence of feeding frequency upon juvenile Tanner crab growth, while the second examined the influence of diet quality, in terms of lipid content, upon growth. C2 stage (2nd crab stage) Tanner crabs (4.2 to 5.6 mm CW) were collected from Kodiak embayments during July 2013. After live-shipment to the Hatfield Marine Science Center in Newport, OR, crabs were placed into individual growth cells immersed in temperature controlled flow-through seawater baths (for details see Ryer et al. 2016). Briefly, growth cells were 3 mm mesh tubes (10 cm diameter) with one closed mesh end. Growth cells were pushed down into the fine sand lining the bottom of the water bath, closed end down. The open end of the growth cell protruded above the water level and was lined with a smooth PVC ring which prevented crabs from climbing out of the cell. Individual C2 crabs were placed in cells at 9°C and fed daily with a gelatinized food. Food was a blended combination of 175 g of cod fillets, 15 g freeze-dried krill, 7.5 g cod liver oil (Everest Nutrition), 7.5 g krill oil (Everest Nutrition), 10 g commercial amino acid supplement (Amino Fuel; Twin Lab), 10 ml algal paste (RotiGrow Plus; Reed Aquiculture), 1 commercial vitamin capsule (Multi Complete, 1.3 g; Nature Made), 15 g commercial calcium supplement (Nature Made), 25 g gelatin powder (Know, Heinz Foods) and 200 ml hot seawater. The mixture was blended to uniform consistency, then 50 g coarse sand was blended in to achieve negative buoyancy. The mixture was poured out into petri dishes, allowed to cool and then frozen until needed. Prior to feeding, the gel food was thawed and minced into fine pieces using a scalpel.

When feeding crabs, each individual was given a quantity of food that, based upon our experience,

was larger than what the crab could consume in a 24 h period. Food that remained from a prior day was removed before any new food was provided. When each crab molted to C3 stage, it was measured using digital photography. At this point, food quantity and food quality experiments were commenced. For the food quantity experiment, crabs were fed either once weekly (Wednesday), 3 times (Monday, Wednesday, Friday) or 7 d a week. For the food quality experiments, crabs were fed either the standard gel food described above (medium lipid), a gel food with no added cod liver or krill oil (low lipid) or a gel food with double the added oil (high lipid: 15 g cod liver oil and 15 g krill oil; Table 2). For both experiments, each treatment was initiated with 10 replicate crabs. Growth cells, and hence crabs, were randomized into 6 water baths, and re-randomized on a weekly basis to preclude any tank effects. All 6 water baths were provided with continuous flow-through seawater (~33 psu) at 9 ± 1°C. Crabs were visually checked daily, and dates of molting recorded. Crabs were re-measured 2 to 5 d after molting. The delay helped ensure that crab exoskeletons were hard enough to resist damage and limb loss during handling. Crabs were reared in this manner until they reached the mid-point (days) between the C5 and C6 stages. This estimate was based upon prior data on the relative increase in intermolt periods from one stage to the next (C. Ryer unpubl. data), as well as the individual growth trajectory of each crab. A randomly chosen subsample of 6 crabs from each treatment in each experiment was measured, weighed and placed in a sealed vial with 2 ml of chloroform under a layer of nitrogen and frozen (−20°C) for later lipid extraction (<1 mo). For both experiments, intermolt periods, from C3 to C4 and C4 to C5, as well as molt increments, i.e. percent increase in carapace width from one stage to the next, were analyzed to test for treatment effects. Where raw or log-transformed data met the assumptions of normality and homoscedasticity, standard ANOVA was used, otherwise non-parametric Kruskal-Wallis ANOVA was used.

Table 2. Total lipids and lipid class composition of low, medium and high lipid diets used in the Tanner crab laboratory feeding experiments. WWT: wet weight

	Low lipid diet	Medium lipid diet	High lipid diet
Total lipids per WWT (mg g^{-1})	7.48 ± 0.55	23.68 ± 0.16	41.11 ± 2.8
% Triacylglycerols	25.33 ± 4.02	64.66 ± 0.46	52.50 ± 7.11
% Free fatty acids	24.53 ± 2.10	6.86 ± 0.08	14.07 ± 0.45
% Sterols	4.83 ± 0.43	4.41 ± 0.02	5.25 ± 0.26
% Phospholipids	36.06 ± 10.58	21.37 ± 0.61	27.82 ± 7.66

Total lipid and lipid class analysis

Whole individual crabs were sampled as detailed above while ~500 mg WWT of sediment and fluff material were processed in each extraction. Fluff samples were centrifuged to settle particulate matter and then excess overlying seawater removed and discarded. Lipids for crabs, sediment and fluff were extracted in chloroform/methanol according to (Parrish 1987) using a modified Folch procedure (Folch et al. 1956). Lipid classes (steryl/wax esters, triacylglyerols, free FAs, sterols, alcohols, acetone mobile polar lipids and phospholipids) were determined using thin layer chromatography with flame ionization detection (TLC/FID) with a MARK VI Iatroscan (Iatron Laboratories) as described by Parrish (1987). The extracts of field-caught crabs, sediments and fluff material were spotted on silica gel coated Chromarods and a 3-stage development system was used to separate lipid classes. The first separations consisted of 25 and 20 min developments in 98.95:1:0.05 hexane:diethyl ether:formic acid. The second separation consisted of a 40 min development in 79:20:1 hexane:diethyl ether:formic acid. The last separation consisted of 15 min developments in 100% acetone followed by 10 min developments in 5:4:1 chloroform:methanol:water. Data peaks were integrated using Peak Simple software v.3.67 (SRI Inc.) and the signal detected (in mV) was quantified using lipid standards (Sigma).

A simplified method for lipid class analyses with a MARK V Iatroscan (Iatron Laboratories) was used for Tanner crabs from the laboratory feeding experiments. Details of the methodology are as in Lu et al. (2008) and Copeman et al. (2017). Briefly, a 3-stage development system was used to separate lipid classes (lipid classes quantified were wax esters, triacylglyerols, free FAs, sterols and polar lipids). The first rod development was in a chloroform: methanol:water solution (5:4:1 by volume) until the leading edge of the solvent phase reached 1 cm above the spotting origin. The rods were then developed in a hexane:diethyl ether: formic acid solution (99:1:0.05) for 48 min and finally rods were developed in a hexane:diethyl ether:formic acid solution (80: 20:0.1) for 38 min. After each solvent development, rods were dried (5 min) and conditioned (5 min) in a constant humidity chamber. Following the last development, rods were scanned

using Peak Simple software and the signal detected in mV was quantified using lipid standards. Lipid classes were expressed both in relative (% of total lipids) and absolute amounts (lipid per WWT, mg g^{-1}).

Fatty acid analysis

Total lipid extracts were transesterified into fatty acid methyl esters (FAMEs) by heating lipids to 85°C for 90 min with 14% boron trifluoride (BF3) in methanol (Morrison & Smith 1964, Budge & Parrish 1999). FAMEs were analyzed on an HP 6890 gas chromatograph (GC) with flame ionization detection (FID) equipped with a 7683 autosampler and a ZB wax+ GC column (Phenomenex). The column was 30 m long, with an internal diameter of 0.32 mm and a 0.25 µm film. The oven temperature began at 65°C for 0.5 min and then the temperature was increased to 195°C (40°C min^{-1}), held for 15 more min, then increased again (2°C min^{-1}) to a final temperature of 220°C. Final temperature was held for 3.25 min. The carrier gas was hydrogen, flowing at 2 ml min^{-1}. Injector temperature started at 150°C and increased (200°C min^{-1}) to a final temperature of 250°C. The detector temperature was constant at 260°C. Peaks were identified using retention times based upon standards purchased from Supelco (37 component FAME, BAME, PUFA 1, PUFA 3). Chromatograms were integrated using Galaxie Chromatography Data System v.1.9.3.2 (Varian).

Statistical analyses of lipid data for crabs from the field

Statistical differences among the lipid parameters of crabs from different nurseries were compared using standard ANOVAs, but when the data failed to meet normality assumptions, we utilized nonparametric Kruskal-Wallis ANOVA. Individual FAs present at >1% in all samples as well as the percentage of bacterial FAs (∑odd and branched chains), the percentage of triacylglycerols (TAGs) and percentage phospholipids (PLs) were included in multivariate analyses using PRIMER v.6 (Primer-E). Together, TAGs and PLs accounted for ~75% of the total lipid classes in juvenile crabs (Table 1). We were not able to perform tissue-specific lipid class analyses due to the small size of these crabs. However, the inclusion of percentage TAGs (neutral lipid storage) and PLs (membrane structures) allowed us to determine FAs that were associated with trophic accumulation and storage of neutral lipids (Copeman & Parrish 2003). To this end, we also included lipid density in our multivariate analyses of crab lipids in order to show FAs that were associated not only with TAGs but also with total lipid density (mg g^{-1}). Qualitative data (% total FA, % lipid classes) were log(x+1) transformed prior to analyses and were then used to calculate a triangular matrix of similarities (Bray-Curtis similarity) between each pair of samples. Non-metric multidimensional scaling (nMDS), an iterative process that uses ranks of similarities, was utilized to explore the effect of nursery site and molt stage on the FA composition of C3 and C4 Tanner crabs.

We completed a 2-way crossed analysis of similarities (ANOSIM) to examine the effect of site and molt stage on lipid composition of juvenile Tanner crabs. The ANOSIM test statistic, R, is a measure of similarity between groups on a scale of 0 to 1. Values between 0.5 and 0.75 indicate that groups are different, but have some degree of overlap, while R > 0.75 indicates well-separated groups (Jaschinski et al. 2011, Kelly & Scheibling 2012). A similarity percentage routine (SIMPER) was used to determine the lipid variables that accounted for the largest portion of the variance between crabs from the Womens and Pillar sites.

RESULTS

The size, weight and condition of recently settled Tanner crabs differed among study sites around Kodiak Island. Age-0 yr crab CWs diverged among sites by August 2010, 2011 and 2012 (Fig. 2; Kruskal-Wallis ANOVA, $p < 0.001$ for each year). In general, crabs were largest at Womens and smallest at Pillar, although the pattern among sites varied slightly among years. During 2010, CW did not differ significantly between Womens and Kalsin ($p > 0.05$), but these crabs were significantly larger than crabs from either Holiday or Pillar ($p < 0.05$), which also did not differ from one another ($p > 0.05$). During both 2011 and 2012, all sites differed significantly in CW, with Womens crabs larger than Kalsin crabs, Kalsin crabs larger than Holiday crabs, and Holiday crabs larger than Pillar crabs ($p < 0.05$ for each).

Among the 2012 crabs from Pillar and Womens, WWTs, DWTs and AFDWTs were each characterized by an exponential relationship to CW (Fig. 3; see legend for statistics). C3 and C4 molt stages were distinct, with crabs <6 mm belonging to the C3 molt stage, and those >6 mm belonging to the C4 molt

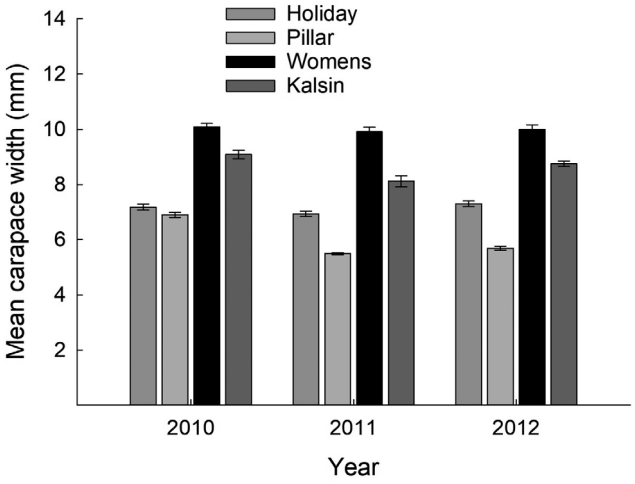

Fig. 2. Mean (±SE) carapace width of age-0 yr Tanner crabs at the 4 study sites during August 2010, 2011 and 2012. Total of 1970 crabs measured

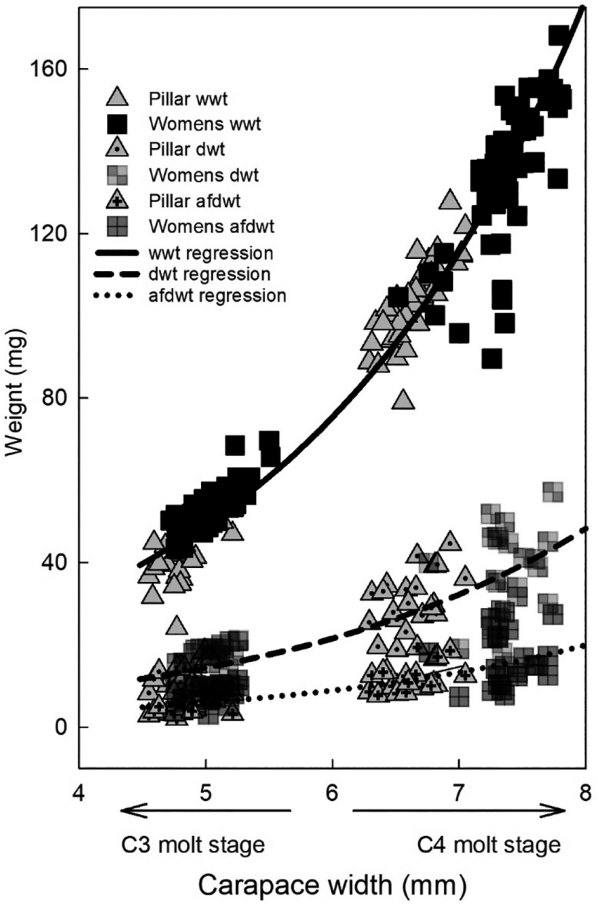

Fig. 3. Plots of Tanner crab wet weight (WWT), dry weight (DWT) and ash-free dry weight (AFDWT) against carapace width (CW). All crabs <6 mm CW were C3 stage (left side of graph), while all >6 mm were C4 stage (right side of graph). Regressions were made on pooled data for C3 and C4 crabs from both Pillar (triangular symbols) and Womens (square symbols). Regression statistics are as follows: log(WWT) = 0.185(CW) + 0.766, r^2 = 0.953; log(DWT) = 0.175(CW) + 0.284, r^2 = 0.679; log(AFDWT) = 0.174(CW) – 0.098, r^2 = 0.578

stage (Fig. 3). However, even within these respective stages, crabs from Womens were on average larger and heavier than those from Pillar. Among C3 crabs, those at Womens had greater CW (t_{69}= –5.91, p < 0.001) and weighed more in terms of WWT (t_{69} = –8.94, p < 0.001), DWT (t_{69} = –5.05, p < 0.001) and AFDWT (Wilcoxon, p < 0.001). This difference between Pillar and Womens was also evident among C4 crabs. Again, those at Womens had greater CW (Wilcoxon p < 0.001) and weighed more in terms of WWT (Wilcoxon p < 0.001), DWT ($t_{36.2}$ = –2.12, p = 0.011) and AFDWT ($t_{38.2}$= –2.58, p = 0.013).

For a given molt stage, crabs at Womens were generally in better morphological-based condition compared to crabs at Pillar. Although the difference was small, mean condition index (logDWT / CW) was significantly higher for crabs from Womens than Pillar (Fig. 4a) among both C3 (Wilcoxon p < 0.001) and C4 ($t_{14.8}$ = 12.71, p = 0.016) stage crabs. A second condition metric, % AFDWT, i.e. the relative amount of crab tissue that was organic in nature (Fig. 4b), also differed between sites. Again, % AFDWT was greater at Womens than at Pillar, among both C3 crabs (Wilcoxon p < 0.001) and C4 crabs (Wilcoxon p < 0.001).

Crabs from Womens and Pillar also differed in lipid content with crabs from Womens having higher total body lipid levels (Fig. 4c; lipid mg g^{-1} WWT). This was statistically demonstrable for both C3 and C4 stage crabs (Kruskal-Wallis ANOVA, p < 0.001 for each). Of the total body lipid, the percentage represented by triacylglycerols (%TAG), dramatically differed between crabs from Womens and Pillar (Fig. 4d). Among both C3 and C4 stage crabs, %TAG was much greater at Womens than at Pillar (Kruskal-Wallis ANOVA, p < 0.001 for each). Of all the condition metrics, %TAG showed the most disparate mean values between crabs from the 2 study sites (Fig. 4a–d).

Juvenile Tanner crabs from Womens and Pillar sites were visualized using nMDS and were spatially segregated based on lipid parameters >1% (Fig. 5). Tests for dissimilarity between the FA and lipid class proportions in Tanner crabs from Womens and Pillar sites and between molt stages revealed that crabs from the 2 different nursery sites were statistically different, with only a small degree of overlap (2-way ANOSIM, global R = 0.662, p = 0.001). There was no significant segregation of crabs by molt stage across nursery sites (R = –0.017, p = 0.63). SIMPER analyses

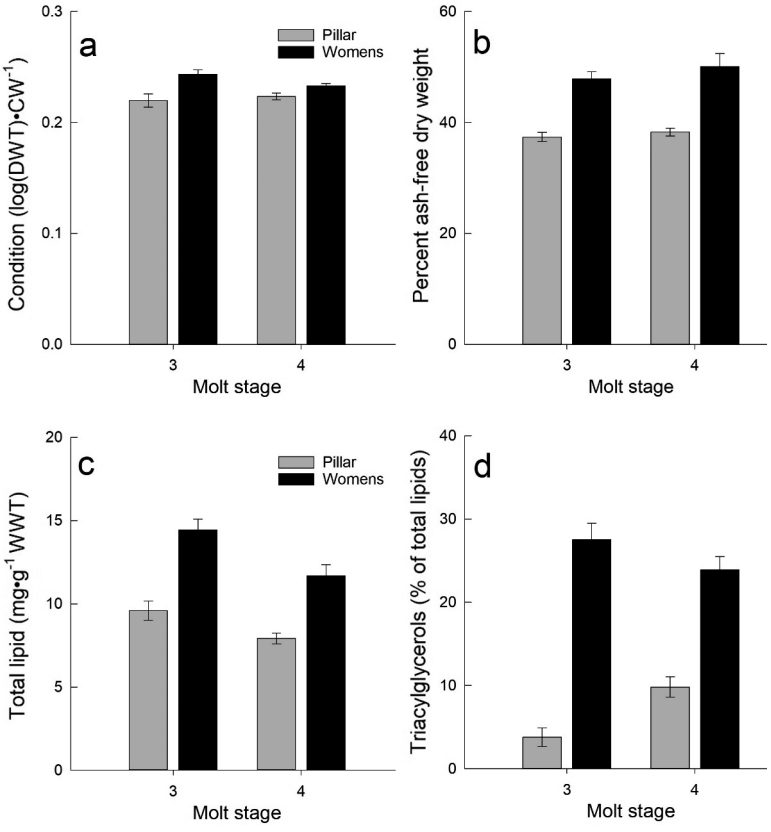

Fig. 4. Mean (±SE) condition metrics for 3rd and 4th molt stage crabs from Pillar and Womens. DWT: dry weight; WWT: wet weight; CW: carapace width. (a) log(DWT) CW^{-1}, n = 174; (b) % ash-free dry weights, n = 174; (c) Mean total lipid (mg g^{-1} WWT), n = 146 and (d) Mean % triacylglycerol (TAG) contribution to total lipid, n = 146

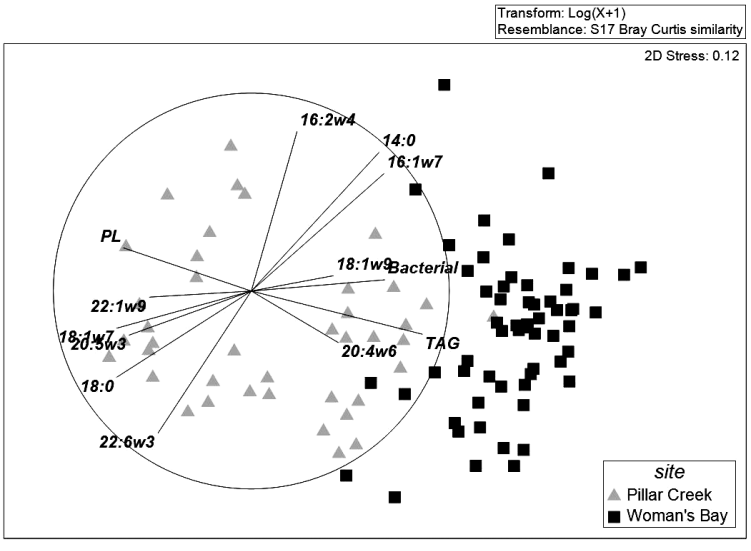

Fig. 5. C3 and C4 Tanner crabs sampled in 2012 from Womens and Pillar sites displayed using non-metric multidimensional scaling (nMDS). ■: crabs from Womens Bay (n = 60); ▲: crabs from Pillar Creek (n = 40). TAG: % triacylglycerols; PL: % phospholipids; bacterial: ∑of the % odd and branched chain fatty acids. Lipid vectors are shown that have a correlation value of >0.6

demonstrated that the top 5 lipid parameters that explained dissimilarity between sites had a cumulative contribution of 79% of the dissimilarity and included, in order of importance, TAG (39.4%), PL (23.2%), 20:5n-3 (6.9%), 16:1n-7 (4.9%) and 22:6n-3 (4.8%).

Sediment characteristics differed appreciably among the 4 study sites (Fig. 6). While all were characterized by relatively coarse sediments at 5 m depth, at 10 m depth and beyond, Womens and Kalsin had finer sediment than Holiday and Pillar (Fig. 6a). Using pooled depth data, the % silt–clay fraction by weight differed among sites (Kruskal-Wallis, $p < 0.001$), being higher at Womens than at either Holiday or Pillar ($p < 0.05$), and higher at Kalsin than at Pillar ($p < 0.05$). The % silt–clay did not differ between Womens and Kalsin, Kalsin and Holiday, or Holiday and Pillar ($p < 0.05$ for each). The % organics by weight (Fig. 6b) also differed between sites (Kruskal-Wallis $p < 0.001$), with differences among nursery means comparable to those seen for the % silt–clay.

The prevalence of FA biomarkers in sediments that were indicative of diatom and bacterial production differed between Pillar and Womens (Fig. 7). The ratio of 16:1n-7/16:0, a biomarker for diatom production (Fig. 7a), was greater in Womens than at Pillar ($F_{1,44}$ = 11.28, p = 0.002). Although this marker was more prevalent in the fluff than in the sediment ($F_{1,44}$ = 21.07, $p < 0.001$), the nursery site effect was consistent in both the fluff and sediment, that is, there was no significant site × sample type (fluff vs. sediment) interaction ($F_{1,44}$ = 0.44, p = 0.511). The prevalence of odd and branched FA chains (∑15:0 + *ai*15:0 + *i*15:0 + 15:1 + *i*16:0 + *ai*16:0 + 17:0 + 17:1), a biomarker for bacterial production (Fig. 7b), was also higher at Womens that at Pillar. However, in this instance, the bacterial marker's contribution to total FAs did not differ between the fluff and sediment ($F_{1,44}$ = 0.92, p = 0.342). Again, there was no significant site × sample type interaction ($F_{1,44}$ = 0.00, p = 0.961).

Our laboratory experiment indicated that food availability (feeding frequency; Fig. 8) and food quality (lipid content; Fig. 9), both

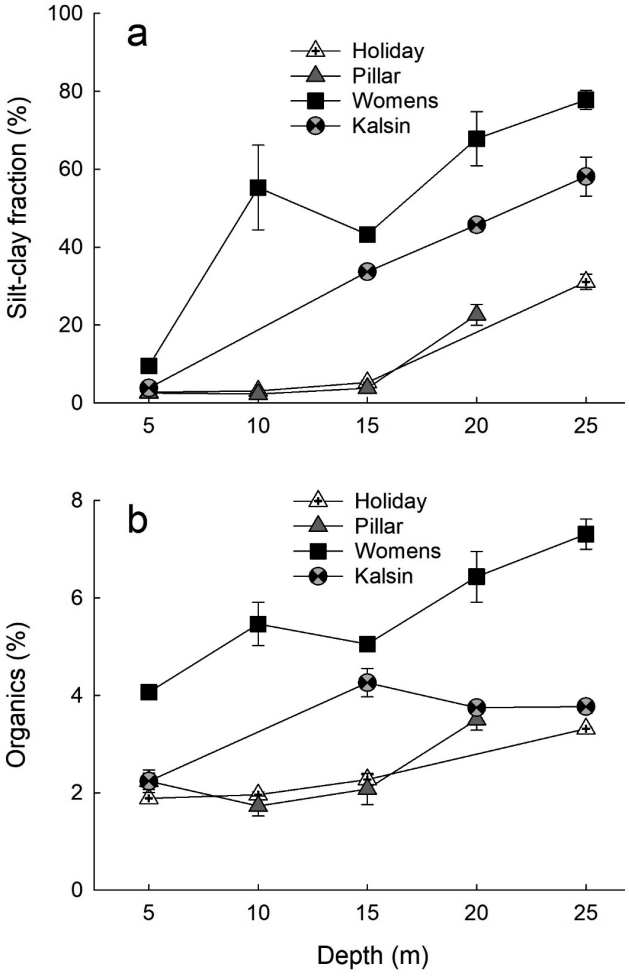

Fig. 6. Mean (±SE) (a) % silt–clay fraction by weight at depths ranging from 5 to 25 m at Holiday, Pillar, Womens and Kalsin study sites; (b) % organic content by weight. Not all depths were sampled for each study site

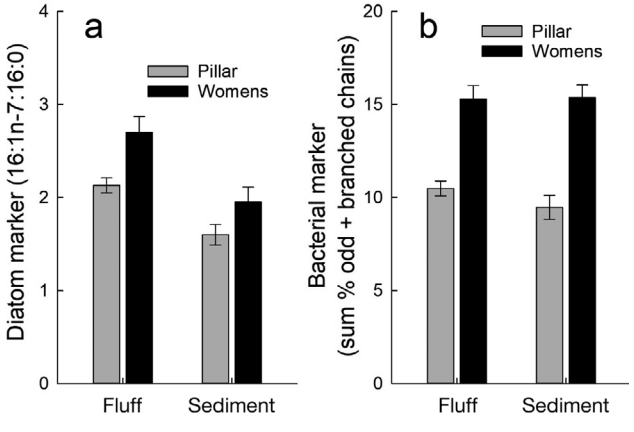

Fig. 7. Mean (±SE) (a) % diatom contribution to total fatty acid profile in fluff and sediment at Pillar and Womens study sites and (b) % bacterial contribution (∑15:0 + *ai*15:0 + *i*15:0 + 15:1 + *i*16:0 + *ai*16:0 + 17:0 + 17:1). Samples were from water depths of 15 to 20 m

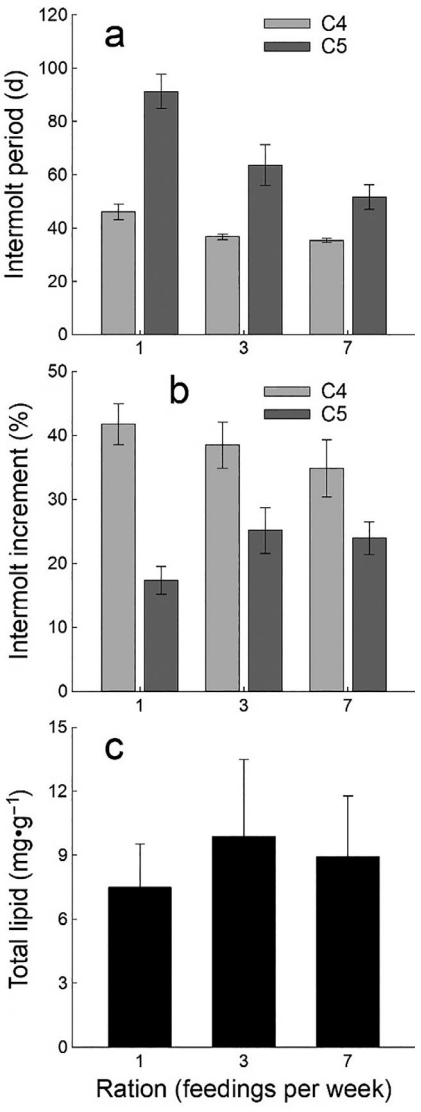

Fig. 8. Mean (±SE) (a) intermolt period in days for C4 and C5 crabs fed a medium lipid diet once, thrice and 7 times weekly; (b) % intermolt increment based on carapace width; (c) total body lipid by weight for C5 crabs, midway through their C5 to C6 intermolt period

influence growth and energy content of juvenile Tanner crabs. Feeding frequency increased the rate at which crabs molted (Fig. 8a), as demonstrated by C4 and C5 intermolt periods (C4: Kruskal-Wallis, $p < 0.001$; C5: Kruskal-Wallis, $p = 0.003$). Among C4 crabs, those being fed once a week had longer intermolt periods ($p < 0.05$) than those fed either 3 times or 7 times weekly, of which the latter two did not differ from one another ($p > 0.05$). Similarly, among C5 crabs, those fed once weekly had longer intermolt periods than those fed 7 times weekly ($p < 0.05$), with those fed 3 times weekly being intermediate and not differing from the other feeding frequencies ($p >$

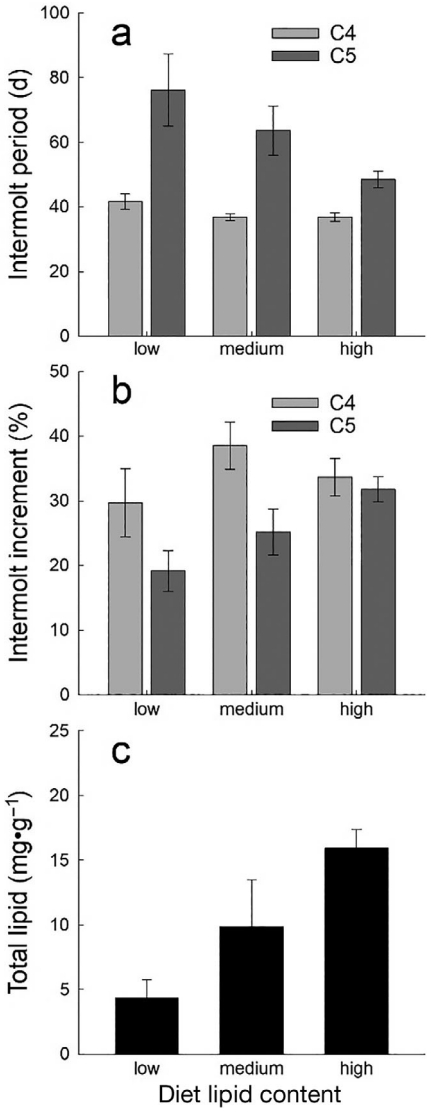

Fig. 9. Mean (±SE) (a) intermolt period in days for C4 and C5 crabs fed a low, medium or high lipid diet, thrice weekly; (b) % intermolt increment based on carapace width; (c) total body lipid by weight for C5 crabs, midway through their C5–C6 intermolt period

0.05). Feeding frequency had no demonstrable effect upon molt increments (Fig. 8b) among either C4 or C5 crabs (C4: $F_{2,21}$ = 0.86, p = 0.438; C5: $F_{2,21}$ = 2.39, p = 0.116). Similarly, feeding frequency had no effect upon body lipid content (Fig. 8c) of crabs that had molted to the C5 stage ($F_{1,8}$ = 3.42, p = 0.101).

Diet quality, in term of lipid content, also influenced growth and the energy density of juvenile Tanner crabs (Fig. 9). Among C4 crabs, intermolt periods (Fig. 9a) tended to be longest, i.e. less frequent molting among crabs on the low lipid diet, although this trend was not statistically significant (Kruskal-Wallis ANOVA, p = 0.095). This influence was, however, more pronounced and statistically significant among C5 crabs (Kruskal-Wallis ANOVA, p = 0.036), such that crabs on the low lipid diet had longer intermolt periods than did those on high lipid diets (p < 0.05). Crabs on the medium lipid diet were intermediate and did not differ between either the low and high lipid diet crabs (p > 0.05). Dietary lipid had no influence on molt increment (Fig. 9b) for C4 crabs ($F_{2,20}$ = 1.22, p = 0.317), but did significantly influence the molt increments of C5 crabs ($F_{2,17}$ = 3.42, p = 0.044). Molt increments were smaller for crabs on the low lipid diet than for those on the high lipid diet (p < 0.05). Molt increments were intermediate on the medium lipid diet, and did not differ from the other 2 diets (p > 0.05). Lastly, dietary lipid had a significant influence upon crab body energy content (Fig. 9c; $F_{2,11}$ = 5.04, p = 0.028). Crabs on the low lipid diet had lower body lipid content than crabs on the high lipid diet (p < 0.05). Crab on the medium lipid diet had intermediate levels of body lipid and did not differ from the other 2 treatments (p > 0.05).

DISCUSSION

Over multiple years we have observed that the size of recently settled Tanner crabs varies considerably between bays around Kodiak Island, Alaska. Among our study sites, crabs are consistently larger at sheltered sites (Womens and Kalsin) than at exposed nurseries (Holiday and Pillar). Potential explanations include differential growth, differing size-dependent predation and differential rates of emigration (Ryer et al. 2015). Here, we tested hypotheses related to the first of these explanations, differential growth. Focusing upon the most disparate of the 4 sites, Pillar and Womens, we demonstrate that age-0 yr crabs are larger (CW) at Womens than at Pillar. As in prior studies, this is partially due to crabs molting more rapidly at Womens, such that at any given time crabs there are characterized by more advanced molt stages (Ryer et al. 2015). However, even for a given molt stage, crabs at Womens were still larger than crabs from Pillar. Further, once standardized for size (CW), Womens crabs were generally in better condition, both in terms of DWT and % AFDWT, than crabs at Pillar. Finally, crabs collected at Womens accumulated more dry biomass and specifically organic mass in the form of high-energy lipids than crabs from Pillar. Using a FA biomarker approach, we found that higher conditioned crabs from sheltered bays were characterized by their accumulation of lipids from diatom and bacterial origins.

We have observed that Womens and Kalsin nursery sites are protected from waves coming in off the Gulf of Alaska, while Holiday and Pillar are more exposed. Our data on sediment grain size is indicative of a lower energy bottom at Womens than at Pillar. Anecdotal observations by divers also indicated that sediments are finer at the more protected sites, which had a thick fluff layer on top of the sediments. We reasoned that the finer sediments are a consequence of a lower energy environment, which also facilitated the retention of phytoplankton settling from the water column. Both grain size and wave exposure are reliable predictors of total benthic biomass for sedimentary shores and rocky shores, respectively (McQuaid & Branch 1984, Ricciardi & Bourget 1999). A greater transfer of water column productivity to the seafloor should support a more diverse and abundant infaunal and epibenthic community (Cammen 1982, Grebmeier et al. 2015), which in turn would support larger predators such as Tanner crabs.

Our contention that larger crab body size and higher lipid storage at protected sites is a consequence of more and/or higher quality food is supported by the sediment characteristics at our study sites. All nearshore sediments receive organic matter from a variety of sources that include fresh phytoplankton, benthic production and terrestrial run-off (Kharlamenko et al. 2001, Spilmont et al. 2009, Schmidt et al. 2010). The trend of increased labile lipids (i.e. total PUFAs) in fluff samples compared to cores is expected, as considerable breakdown of freshly deposited sedimentary material likely occurs over time (Copeman & Parrish 2003). Canuel & Martens (1996) demonstrated that rates of FA degradation were higher in the top 1.25 cm than those below 3.5 cm in sediments collected at Cape Lookout Bight, North Carolina. Results indicate that not only did our protected sites have finer sediment, but they were also higher in organic content, particularly in the case of Womens, where growth was consistently highest. Higher organic content is typical of lower energy environments with finer sediments (Ricciardi & Bourget 1999), since low density organic materials are not continually suspended or transported offshore. In preparing sediment samples for organic analysis, we excluded large, easily observed macrofauna (large polychaetes, amphipods, isopods, clams, shrimp, etc.) as well as easily identifiable pieces of detrital material, e.g. bits of kelp and algae. Thus, the remaining organic matter represented the smaller macrofauna, meiofauna, microalgae, fine detritus and associated micro-organisms, which likely constitutes the diet of age-0 yr Tanner crabs.

Both sediments and crabs at sheltered sites had higher lipids per WWT than at exposed sites. Lipids are energetically rich compounds that have a wide diversity of structures in marine food webs (Parrish 1988). They are abundant in animals from cold and seasonal environments and they provide the densest form of energy, with over two-thirds more energy per gram than proteins or carbohydrates (Parrish 1988). Storage of lipids in high latitude organisms is considered an adaptation to prolonged overwintering periods when feeding activity may be severely reduced (Sogard 1997, Kattner et al. 2007). Relatively few studies have measured total lipids and lipid classes in the juvenile stages of cold-water crabs. However, previous field efforts in the near-shore cold waters of Labrador, Canada did examine the lipid composition of both hermit crabs *Pagurus* sp. and toad crabs *Hyas coarctatus* and found them to have total lipids per WWT of 14 and 3 mg g^{-1}, respectively (Copeman & Parrish 2004). Further, wild-caught juvenile red king crabs from southeast Alaska ranged in lipid densities from 5 to 12 mg g^{-1} WWT during the C2 to the C4 stages of development (Copeman et al. 2012). We measured total lipid densities within this range, as Tanner crabs had on average 8 to 14 mg g^{-1} depending on their sampling location but not their molt stage.

The 3 major lipid classes in juvenile Alaskan crabs are TAGs, sterols (STs) and PLs (Copeman et al. 2012, Stoner et al. 2013). Much of the changes in total lipid density in Tanner crabs was due to the accumulation of TAGs, with higher levels in Womens crabs (>25%) than in Pillar crabs (<10%). Numerous studies have demonstrated that higher proportions of TAGs are associated with better growth, survival and molting success in early life stages of marine invertebrates (Copeman et al. 2012, Stoner et al. 2013, Connelly et al. 2014, Beder 2015) and better growth and swimming capability in juvenile fish (Copeman & Laurel 2010, Litz et al. 2017). Higher energy reserves, all other things being equal, are typically indicative of animals that have access to either better quality food (Catacutan 2002, Hu et al. 2017) or a greater quantity of food (Andres et al. 2007, McLean & Todgham 2015). Juvenile Tanner crabs within our laboratory experiments responded to both of these dietary parameters by storing higher lipids per WWT in the form of neutral storage lipids, TAGs.

For juvenile and larval crustaceans, dietary lipids are important factors in improving growth and molting success (Xu et al. 1994, Wen et al. 2006, Glencross 2009, Tziouveli & Smith 2012). However, there is sparse literature on lipid metabolism of cold-water

juvenile crabs in the North Pacific. Crabs experience discontinuous growth by molting (ecdysis), with their growth otherwise constrained by a rigid exoskeleton (Sánchez-Paz et al. 2006). Copeman et al. (2012) did examine the changes in proximate composition and lipids throughout a complete intra-molt cycle (C4 to C5) in red king crab *Paralithodes camtschaticus* juveniles. They found 3 distinct phases of lipid accumulation throughout the molt cycle. The first stage, post-molt, only lasted a few days and was characterized by crabs with soft, pale bodies that had low lipid levels and high water content. The second phase, intra-molt, was defined by rapid accumulation of lipids and higher feeding rates while the last stage, pre-molt, was characterized by reduced feeding behavior and low lipid accumulation. This tri-modal lipid accumulation pattern observed in red king crabs from Alaska was similar to that previously reported in other invertebrates such as shrimp (Ouellet et al. 1992) and in older life history stages of crabs (Zhou et al. 1998). Here, we observed a similar pattern in the feeding behavior of juvenile Tanner crabs in our laboratory experiments. Due to variation in lipids throughout the molt cycle, Copeman et al. (2012) suggested that caution should be taken when comparing the condition of crabs from the field, given their indeterminate intra-molt status. Therefore, we avoided sampling any wild Tanner crabs that were pale or soft in appearance, and our sample sizes were large enough that it is unlikely that molt status may have affected the consistent differences between crabs from different nursery embayments. Further, throughout our laboratory experiments, we only sampled crabs at a standardized mid-molt period to control for variation in lipids throughout the molt cycle.

We are uncertain of the importance of lipid storage to overwintering survival of cold-water juvenile crabs. In many boreal groundfish species (i.e. Pacific cod *Gadus macrocephalus* and walleye pollock *Gadus chalcogrammus*), lipids accumulate during the summer in the liver and play a vital role in overwintering survival. Increased recruitment of North Pacific fish has been observed in cold years, when elevated fish condition during the late larval and early juvenile phases is positively correlated with matches in the abundance and distribution of large cold-water, high-fat zooplankton species (Beaugrand & Kirby 2010, Heintz et al. 2013, Siddon et al. 2013a,b, Sigler et al. 2016). Thus, late summer has been proposed as a critical period for boreal fish as they must store enough energy or face high overwintering mortality. Tanner crab juveniles feed on the benthos and are likely generalists, consuming both detrital and infaunal invertebrates. Therefore, it is likely that the seasonality of food availability for Tanner crab is much less variable than for juvenile groundfish. However, during non-feeding early life-history stages of Alaskan crabs, such as the glaucothoe stage of red king crabs, survival has been correlated with sufficient storage of TAGs observed in the form of microscopic lipid droplets (Beder 2015). In addition, the incidence of molt-death syndrome is common in other species of crab reared on diets with inadequate lipid, cholesterol or PUFAs (Holme et al. 2007, Wu et al. 2014, Han et al. 2015). Therefore, increased lipid storage both in fish and crabs is associated with higher growth and resistance to starvation. However, further research is required to determine if lipid storage prior to overwintering affects winter growth and later recruitment into adult cold-water crab populations.

The diet of adult Tanner crabs has not been well described. However, Tanner crab adults were examined near Kodiak Island, and the 3 major prey items for crabs >40 mm in CW were crabs, fish and mollusks, while crabs <40 mm in CW consumed bivalves, fish, decapod crustaceans, polychaetes and sediments (Jewett & Feder 1983). This is in agreement with studies on Arctic snow crab *Chionoecetes opilio* that reported major prey items to include polychaetes, decapod crustaceans, echinoderms and mollusks (Divine et al. 2017). However, the largest crabs in our study were 10 mm in CW, and much less is known about the diet of recently settled Tanner crabs. One study on the food of post-larval king crab *Paralithodes camtschatica* in southern Alaska found a high dietary incidence of occurrence for sediments (93%) (Feder et al. 1980). This indicated that sedimentary feeding is common in newly settled crabs. Further, diatom fragments were found in 27% of king crab stomachs and most of the diatoms were identified as pelagic rather than benthic in origin, indicating the importance of pelagic–benthic coupling for newly settled crab nutrition (Feder et al. 1980). Juvenile stages of the southern king crab *Lithodes santolla* in the San Jorge Gulf, Argentina, showed high reliance on red algae, ophiuroids, isopods, polychaete worms and bryozoans (Vinuesa et al. 2013), with unidentified organic remains being the most common prey item. This finding is in agreement with observations on the feeding behavior of similarly sized juvenile Alaskan red king crabs, where Pirtle & Stoner (2010) recorded juvenile crabs removing the soft tissue of hydroids and bryozoans without ingesting the capsule or theca. Based on the above observations of cold-water newly settled crab diets, we

assume that juvenile Tanner crabs are generalists, consuming a wide variety of small infaunal organisms as well as detrital material that is found on the sediment–water interface.

It is probable that the ontogenetic stage of crab development plays an important role in the utility of different methods of diet determination. Kolts et al. (2013) examined the relative value of stomach contents, stable isotopes and FAs for determining diet in northern adult Bering Sea snow crab and concluded that stomach contents yielded the most definitive diet information. However, they noted that this was true because larger crabs (40 mm CW) eat prey that mostly contained hard, easily identifiable structures. This is not the case for small juvenile crabs such as those in this study (4 to 8 mm CW) that have stomach contents typified by unidentified organic remains (authors' pers. obs.), making the FA biomarker approach more attractive.

FAs are important components of acyl lipid classes (i.e. TAGs and PLs) and are now commonly used in marine ecology studies to determine dietary sources (Kelly & Scheibling 2012, Parrish 2013). The use of proportional FA data derived from the total lipid pool should be approached with caution. Here, we also present complementary data on total lipids per WWT and the lipid class composition (i.e. %TAG and %PL) of crabs. The addition of these data allow us to interpret biomarkers as those associated with excess dietary energy storage (i.e. TAGs) versus those associated with membrane structure and function (i.e. PLs). This is demonstrated in multivariate space with crabs from Womens having higher total lipids and %TAG clustered with elevated diatom and bacterial FA markers. Oppositely, Pillar crabs that had relatively higher proportion of PLs and lower total lipids were associated with elevated 22:6n-3 and 18:0. These 2 FAs are often indicative of the molecular-species composition of PLs in marine fish and invertebrates (Bell & Dick 1991, MacPherson et al. 1998), and the directionality of these FAs do not indicate a higher dietary proportion but rather less bacterial and diatom FA accumulation in the TAG reserves of crabs from Pillar.

The FA biomarker approach has previously been used to determine crab diets in warm mangroves (Meziane & Tsuchiya 2000, Hall et al. 2006, Meziane et al. 2006), seagrass systems (Alfaro et al. 2006, Canuel et al. 2007) and cold-water sub-photic zones (Galloway et al. 2013, Kolts et al. 2013). However, this study is the first to examine the dietary patterns in juvenile crabs from cold boreal systems. Similar to other recent studies in seasonally pulsed environments (Copeman et al. 2016, Bosley et al. 2017, Miller et al. 2017), we found that diatoms are important to the energy storage of juvenile crabs. Recent criticism of the use of FA biomarkers in benthic studies has been due to the complexity of dietary sources in benthic food webs, the ability of benthic consumers to modify dietary FAs and the relative lack of truly unique FA trophic markers (Kelly & Scheibling 2012, Kolts et al. 2013). For this reason, we focused on the utility of 2 well established FA markers for diatoms (16:1n-7/16:0) and bacteria (∑odd and branched chains) (Claustre et al. 1988, Viso & Marty 1993, Dalsgaard et al. 2003, Kelly & Scheibling 2012, Parrish 2013, Galloway & Winder 2015, Bosley et al. 2017).

Previous trophodynamic studies on crabs have also found high dietary representation from diatoms and bacteria as is typical of invertebrates that feed on benthic organic debris (Copeman & Parrish 2003, Alfaro et al. 2006, Spilmont et al. 2009, Bosley et al. 2017). From a FA biomarker perspective, we cannot separate this diatom signal into benthic versus pelagic production. Although Parrish et al. (1995) did find a strong correlation between 16:1n-7/16:0 and pelagic centric diatoms that was not present for either pennate or benthic diatom production. Given the depth of our crab collections (10 to 30 m), we conclude that most of this production originated in the pelagic zone and had settled to the benthos. The addition of bulk $\delta^{15}N$ to FA trophic studies can improve information on dietary pathways from primary producers to secondary consumers. This is because $\delta^{15}N$ indicates trophic position in food webs, as $\delta^{15}N$ is assumed to become enriched by a mean of ~3.4‰ with each trophic level (Deniro & Epstein 1981). Spilmont et al. (2009) used this dual biomarker approach to investigate the diet of soldier crabs *Mictyris longicarpus* in an Australian sand bank and also found that bacteria and diatoms constituted the base of its diet. However, the $\delta^{15}N$ isotopic signatures of the crabs in their study suggested that meiofauna represented an intermediate link between crabs and diatom/bacterial production. This is likely also the case for juvenile Tanner crabs, with previous studies in our nursery sites showing a high co-occurrence between dense lawns of ampharetid polychaetes *Sabellides sibirica* and juvenile Tanner crabs and Alaskan flatfish (Laurel et al. 2012, Ryer et al. 2015).

While food quality/quantity would appear to play a substantial role in the growth-related size disparity between crabs at our study sites, there are other non-mutually exclusive explanations. We previously considered the possibility that temperature, a principal driver of growth in poikilotherms (Ryer et al. 2015), might be driving differences in growth between

sites; however, we concluded that the small differences in temperature between sites (<0.5°C), as well as the pattern of differences (Womens > Pillar > Holiday > Kalsin), did not support a principal role for temperature (Ryer et al. 2015). We also considered differential size-dependent predation, positing that disproportional predation on smaller crabs would skew size distributions towards the larger size at high-predation sites. Settlement is complete by July around Kodiak, and crab densities from July to August remained relatively constant at Womens and Kalsin, while densities at Pillar and Holiday declined. This pattern runs contrary to expectations under a differential size-dependent predation hypothesis. However, it is consistent with another possible mechanism: differential off-shore movements as crabs increase in size. It is difficult to imagine newly settled Tanner crabs moving extensive distances. If, however, after several molts crabs began moving to seek out more favorable habitat, this could result in crabs at Pillar and Holiday moving offshore to deeper water and finer sediments. This would skew the size-distribution towards smaller crabs. In contrast, at Womens and Kalsin, where sediments are already relatively fine, crabs might be more inclined to stay put, contributing to the observed difference in size distributions between sites. Although our sediment data from the field as well as our laboratory experiment both indicate a potential for higher growth at sites with fine sediment, our distributional data on crabs cannot eliminate differential migration as a potential co-contributor to the observed size pattern in crabs.

While there is a general understanding that adult Tanner crabs are typically found in association with relatively fine sediments (Zhou & Shirley 1997), there has been scant information on habitat associations and habitat quality for recently settled Tanner crabs (Rosenkranz et al. 1998, Nielsen et al. 2007). In the shallow-water embayment around Kodiak Island, Alaska, where high summer temperatures can accelerate growth, the availability of adequate nutrition appears to limit growth in some habitats. Embayments with fine sediments, associated with low wave energy, appear to support more rapid crab growth due to an influx of labile organic materials. In particular, we determined that lipids associated with diatom production were associated with more rapid crab growth. These finding were supported by laboratory experiments demonstrating that high lipid diets result in shortened intermolt periods as well as greater incremental growth associated with each molt. These findings indicate that availability of primary production, as well as favorable mechanisms that allow for its accumulation and incorporation into the benthic food web, can control the quality of habitat for newly settle Tanner crabs. While these findings further our understanding of juvenile Tanner crab habitat in shallow water, they may also have applicability for elucidating how annual variation in the intensity and location of phytoplankton blooms (Sigler et al. 2016) may modulate habitat quality for the Tanner crab throughout its range.

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LITERATURE CITED

Alfaro AC, Thomas F, Sergent L, Duxbury M (2006) Identification of trophic interactions within an estuarine food web (northern New Zealand) using fatty acid biomarkers and stable isotopes. Estuar Coast Shelf Sci 70:271–286

Andres M, Estevez A, Rotllant G (2007) Growth, survival and biochemical composition of spider crab *Maja brachydactyla* (Balss, 1922) (Decapoda: Majidae) larvae reared under different stocking densities, prey:larva ratios and diets. Aquaculture 273:494–502

Armstrong J, Armstrong D, Hilborn R (1998) Crustacean resources are vulnerable to serial depletion—the multifaceted decline of crab and shrimp fisheries in the greater Gulf of Alaska. Rev Fish Biol Fish 8:117–176

Beaugrand G, Kirby RR (2010) Climate, plankton and cod. Glob Change Biol 16:1268–1280

Beder A (2015) The effects of dietary essential fatty acid enrichment on the nutrition and condition of red king crab (*Paralithodes camtschaticus*) larvae. MSc thesis, University of Alaska, Fairbanks, AK

Bell MV, Dick JR (1991) Molecular species composition of the major diacyl glycerophospholipids from muscle, liver, retina and brain of cod (*Gadus morhua*). Lipids 26: 565–573

Bosley KM, Copeman LA, Dumbauld BR, Bosley KL (2017) Identification of burrowing shrimp food sources along an estuarine gradient using fatty acid analysis and stable isotope ratios. Estuaries Coasts 40:1113–1130

Budge SM, Parrish CC (1998) Lipid biogeochemistry of plankton, settling matter and sediments in Trinity Bay, Newfoundland. II. Fatty acids. Org Geochem 29: 1547–1559

Budge SM, Parrish CC (1999) Lipid class and fatty acid composition of *Pseudo-nitzschia multiseries* and *Pseudo-nitzschia pungens* and effects of lipolytic enzyme deactivation. Phytochemistry 52:561–566

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar Mamm Sci 22:759–801

Cammen LM (1982) Effect of particle size on organic content and microbial abundance within four marine sediments. Limnol Oceanogr 9:509–518

Canuel EA, Martens CS (1996) Reactivity of recently deposited organic matter: degradation of lipid compounds near the sediment-water interface. Geochim Cosmochim Acta 60:1793–1806

Canuel EA, Spivak AC, Waterson EJ, Duffy JE (2007) Biodiversity and food web structure influence short-term accumulation of sediment organic matter in an experimental seagrass system. Limnol Oceanogr 52: 590–602

Catacutan MR (2002) Growth and body composition of juvenile mud crab, *Scylla serrata*, fed different dietary protein and lipid levels and protein to energy ratios. Aquaculture 208:113–123

Claustre H, Marty JC, Cassiani L, Dagaut J (1988) Fatty acid dynamics in phytoplankton and microzooplankton communities during a spring bloom in the coastal Ligurian Sea: ecological implications. Mar Microb Food Webs 3: 51–66

Connelly TL, Deibel D, Parrish CC (2014) Trophic interactions in the benthic boundary layer of the Beaufort Sea shelf, Arctic Ocean: combining bulk stable isotope and fatty acid signatures. Prog Oceanogr 120:79–92

Copeman LA, Laurel BJ (2010) Experimental evidence of fatty acid limited growth and survival in Pacific cod larvae. Mar Ecol Prog Ser 412:259–272

Copeman LA, Parrish CC (2003) Marine lipids in a cold coastal ecosystem: Gilbert Bay, Labrador. Mar Biol 143: 1213–1227

Copeman LA, Parrish CC (2004) Lipids classes, fatty acids, and sterols in seafood from Gilbert Bay, southern Labrador. J Agric Food Chem 52:4872–4881

Copeman LA, Parrish CC, Gregory RS, Jamieson RE, Wells J, Whiticar MJ (2009) Fatty acid biomarkers in coldwater eelgrass meadows: elevated terrestrial input to the food web of age-0 Atlantic cod *Gadus morhua.* Mar Ecol Prog Ser 386:237–251

Copeman LA, Stoner AW, Ottmar ML, Daly B, Parrish CC, Eckert GL (2012) Total lipids, lipid classes, and fatty acids of newly settled red king crab (*Paralithodes camtschaticus*): comparison of hatchery-cultured and wild crabs. J Shellfish Res 31:153–165

Copeman LA, Laurel BJ, Boswell KM, Sremba AL and others (2016) Ontogenetic and spatial variability in trophic biomarkers of juvenile saffron cod (*Eleginus gracilis*) from the Beaufort, Chukchi and Bering Seas. Polar Biol 39:1109–1126

Copeman LA, Laurel BJ, Spencer M, Sremba A (2017) Temperature impacts on lipid allocation among juvenile gadid species at the Pacific Arctic-Boreal interface: an experimental laboratory approach. Mar Ecol Prog Ser 566:183–198

Dalsgaard J, St John M, Kattner G, Muller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225–340

Daly B, Long WC (2014) Inter-cohort cannibalism of early benthic phase blue king crabs (*Paralithodes platypus*): alternate foraging strategies in different habitats lead to different functional responses. PLOS ONE 9:e88694

Deniro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:341–351

Divine LM, Bluhm BA, Mueter FJ, Iken K (2017) Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and $\delta^{13}C$ and $\delta^{15}N$ stable isotopes. Deep Sea Res II 135:124–136

Feder HM, McCumby K, Paul AJ (1980) The food of post-larval king crab, *Paralithodes camtschatica*, in Kachemak Bay, Alaska (Decapoda, Lithodidae). Crustaceana 39: 315–318

Folch J, Less M, Sloane Stanley GH (1956) A simple method for the isolation and purification of total lipids from animal tissues. J Biol Chem 22:497–509

Fong KH, Dunham JS (2007) Inshore Tanner crab (*Chionoecetes bairdi*) biology in a central coast inlet, British Columbia, Canada. J Shellfish Res 26:581–595

Galloway AWE, Winder M (2015) Partitioning the relative importance of phylogeny and environmental conditions on phytoplankton fatty acids. PLOS ONE 10:e0130053

Galloway AWE, Lowe AT, Sosik EA, Yeung JS, Duggins DO (2013) Fatty acid and stable isotope biomarkers suggest microbe-induced differences in benthic food webs between depths. Limnol Oceanogr 58:1451–1462

Galloway AWE, Eisenlord ME, Dethier MN, Holtgrieve GW, Brett MT (2014) Quantitative estimates of isopod resource utilization using a Bayesian fatty acid mixing model. Mar Ecol Prog Ser 507:219–232

Glencross BD (2009) Exploring the nutritional demand for essential fatty acids by aquaculture species. Rev Aquacult 1:71–124

Grebmeier JM (1993) Studies of pelagic–benthic coupling extended onto the Soviet continental shelf in the Northern Bering and Chukchi seas. Cont Shelf Res 13:653–668

Grebmeier JM, Bluhm BA, Cooper LW, Danielson SL and others (2015) Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. Prog Oceanogr 136:92–114

Hall D, Lee SY, Meziane T (2006) Fatty acids as trophic tracers in an experimental estuarine food chain: tracer transfer. J Exp Mar Biol Ecol 336:42–53

Han T, Wang JT, Li XY, Yang YX and others (2015) Effects of dietary cholesterol levels on the growth, molt performance, and immunity of juvenile swimming crab, *Portunus trituberculatus.* Isr J Aquacult Bamidgeh 67:1–11

Hargrave BT (1972) Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. Limnol Oceanogr 17:583–586

Hartnoll RG (2001) Growth in Crustacea—twenty years on. Hydrobiologia 449:111–122

Heintz RA, Siddon EC, Farley EV, Napp JM (2013) Correlation between recruitment and fall condition of age-0 pollock (*Theragra chalcogramma*) from the eastern Bering Sea under varying climate conditions. Deep Sea Res II 94:150–156

Holme MH, Southgate PC, Zeng C (2007) Survival, development and growth response of mud crab, *Scylla serrata*, megalopae fed semi-purified diets containing various fish oil:corn oil ratios. Aquaculture 269:427–435

Hu SX, Wang JT, Han T, Li XY, Jiang YD, Wang CL (2017) Effects of dietary DHA/EPA ratios on growth performance, survival and fatty acid composition of juvenile swimming crab (*Portunus trituberculatus*). Aquacult Res 48:1291–1301

Jaschinski S, Brepohl DC, Sommer U (2011) Seasonal variation in carbon sources of mesograzers and small predators in an eelgrass community: stable isotope and fatty acid analyses. Mar Ecol Prog Ser 431:69–82

Jewett SC, Feder M (1983) Food of the Tanner crab *Chionoecetes bairdi* near Kodiak Island, Alaska. J Crustac Biol 3:196–207

Kattner G, Hagen W, Lee RF, Campbell R and others (2007) Perspectives on marine zooplankton lipids. Can J Fish Aquat Sci 64:1628–1639

Kelly JR, Scheibling RE (2012) Fatty acids as dietary tracers in benthic food webs. Mar Ecol Prog Ser 446:1–22

Kharlamenko VI, Kiyashko SI, Imbs AB, Vyshkvartzev DI (2001) Identification of food sources of invertebrates from the seagrass *Zostera marina* community using carbon and sulfur stable isotope ratio and fatty acid analyses. Mar Ecol Prog Ser 220:103–117

Kolts JM, Lovvorn JR, North CA, Grebmeier JM, Cooper LW (2013) Relative value of stomach contents, stable isotopes, and fatty acids as diet indicators for a dominant invertebrate predator (*Chionoecetes opilio*) in the northern Bering Sea. J Exp Mar Biol Ecol 449:274–283

Laurel BJ, Ryer CH, Spencer M, Iseri P, Knoth B, Stoner A (2012) Effects of natural and anthropogenic disturbance on polychaete worm tubes and age-0 flatfish distribution. Mar Ecol Prog Ser 466:193–203

Litz MNC, Miller JA, Copeman LA, Hurst TP (2017) Effects of dietary fatty acids on juvenile salmon growth, biochemistry, and aerobic performance: a laboratory rearing experiment. J Exp Mar Biol Ecol 494:20–31

Longbottom M (1970) The distribution of *Arenicola marina* (L.) with particular reference to the effects of particle size and organic matter of the sediments. J Exp Mar Biol Ecol 5:138–157

Lu YH, Ludsin SA, Fanslow DL, Pothoven SA (2008) Comparison of three microquantity techniques for measuring total lipids in fish. Can J Fish Aquat Sci 65:2233–2241

MacPherson JC, Pavlovich JG, Jacobs RS (1998) Phospholipid composition of the granular amebocyte from the horseshoe crab, *Limulus polyphemus.* Lipids 33:931–940

McLean KM, Todgham AE (2015) Effect of food availability on the growth and thermal physiology of juvenile Dungeness crabs (*Metacarcinus magister*). Conserv Physiol 3:cov013

McQuaid CD, Branch GM (1984) Influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. Mar Ecol Prog Ser 19:145–151

Meziane T, Tsuchiya M (2000) Fatty acids as tracers of organic matter in the sediment and food web of a mangrove/intertidal flat ecosystem, Okinawa, Japan. Mar Ecol Prog Ser 200:49–57

Meziane T, d'Agata F, Lee SY (2006) Fate of mangrove organic matter along a subtropical estuary: small-scale exportation and contribution to the food of crab communities. Mar Ecol Prog Ser 312:15–27

Miller JA, Peterson WT, Copeman LA, Du X, Morgan CA, Litz MNC (2017) Temporal variation in the biochemical ecology of lower trophic levels in the Northern California Current. Prog Oceanogr 155:1–12

Morrison WR, Smith LM (1964) Preparation of fatty acid methyl esters and dimethylacetals from lipids with boron fluoride–methanol. J Lipid Res 5:600–608

Nielsen JK, James S, Taggart J, Shirley TC, Mondragon J (2007) Spatial distribution of juvenile and adult female Tannercrabs (*Chionoecetes bairdi*) in a glacial fjord ecosystem: implications for recruitment processes. ICES J Mar Sci 64:1772–1784

Ouellet P, Taggart CT, Frank KT (1992) Lipid condition and survival in shrimp (*Pandalus borealis*) larvae. Can J Fish Aquat Sci 49:368–378

Palacios R, Armstrong DA, Armstrong J, Williams G (1985) Community analysis applied to characterization of blue king crab habitat around the Pribilof Islands. In: Melteff B (ed) Proc Int King Crab Symp, 22–24 January, Anchorage, AK. University of Alaska Sea Grant Report, Fairbanks, AK, p 193–209

Parrish CC (1987) Separation of aquatic lipid classes by chromarod thin-layer chromatography with measurement by Iatroscan flame ionization detection. Can J Fish Aquat Sci 44:722–731

Parrish CC (1988) Dissolved and particulate marine lipid classes: a review. Mar Chem 23:17–40

Parrish CC (1998) Lipid biogeochemistry of plankton, settling matter and sediments in Trinity Bay, Newfoundland. I. Lipid classes. Org Geochem 29:1531–1545

Parrish CC (2013) Lipids in marine ecosystems. ISRN Oceanogr 2013:604045

Parrish CC, McKenzie CH, MacDonald BA, Hatfield EA (1995) Seasonal studies of seston lipids in relation to microplankton species composition and scallop growth in South Broad Cove, Newfoundland. Mar Ecol Prog Ser 129:151–164

Parrish CC, Thompson RJ, Deibel D (2005) Lipid classes and fatty acids in plankton and settling matter during the spring bloom in a cold ocean coastal environment. Mar Ecol Prog Ser 286:57–68

Pirtle JL, Stoner AW (2010) Red king crab (*Paralithodes camtschaticus*) early post-settlement habitat choice: structure, food, and ontogeny. J Exp Mar Biol Ecol 393: 130–137

Ricciardi A, Bourget E (1999) Global patterns of macroinvertebrate biomass in marine intertidal communities. Mar Ecol Prog Ser 185:21–35

Richoux NB, Deibel D, Thompson RJ, Parrish CC (2004) Seasonal changes in the lipids of *Mysis mixta* (Mysidacea) from the hyperbenthos of a cold-ocean environment (Conception Bay, Newfoundland). Can J Fish Aquat Sci 61:1940–1953

Richoux NB, Deibel D, Thompson RJ, Parrish CC (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

Rosenkranz GE, Tyler AV, Kruse GH, Niebauer HJ (1998) Relationship between wind and year class strength of Tanner crabs in the southeastern Bering Sea. Alsk Fish Res Bull 5:18–24

Ryer CH, Long WC, Spencer ML, Iseri P (2015) Depth distribution, habitat associations, and differential growth of newly settled southern Tanner crab (*Chionoecetes bairdi*) in embayments around Kodiak Island, Alaska. Fish Bull (Wash DC) 113:256–269

Ryer CH, Ottmar M, Spencer M, Anderson JD, Cooper D (2016a) Temperature-dependent growth of early juvenile southern Tanner crab *Chionoecetes bairdi*: implications for cold pool effects and climate change in the south eastern Bering Sea. J Shellfish Res 35:259–267

Sánchez-Paz A, García-Carreño F, Muhlia-Almazán A,

Peregrino-Uriarte AB, Hernández-López J, Yepiz-Plascencia G (2006) Usage of energy reserves in crustaceans during starvation: status and future directions. Insect Biochem Mol Biol 36:241–249

Schmidt F, Hinrichs KU, Elvert M (2010) Sources, transport, and partitioning of organic matter at a highly dynamic continental margin. Mar Chem 118:37–55

Siddon EC, Heintz RA, Mueter FJ (2013a) Conceptual model of energy allocation in walleye pollock (*Theragra chalcogramma*) from age-0 to age-1 in the southeastern Bering Sea. Deep Sea Res II 94:140–149

Siddon EC, Kristiansen T, Mueter FJ, Holsman KK, Heintz RA, Farley EV (2013b) Spatial match-mismatch between juvenile fish and prey provides a mechanism for recruitment variability across contrasting climate conditions in the eastern Bering Sea. PLOS ONE 8:e84526

Sigler MF, Napp JM, Stabeno PJ, Heintz RA, Lomas MW, Hunt GL (2016) Variation in annual production of copepods, euphausiids, and juvenile walleye pollock in the southeastern Bering Sea. Deep Sea Res II 134:223–234

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60: 1129–1157

Sokal RR, Rohlf FJ (1969) Biometry: the principles and practice of statistics in biological research. WH Freeman, San Francisco, CA

Spilmont N, Meziane T, Seuront L, Welsh DT (2009) Identification of the food sources of sympatric ghost shrimp (*Trypaea australiensis*) and soldier crab (*Mictyris longicarpus*) populations using a lipid biomarker, dual stable isotope approach. Austral Ecol 34:878–888

St John MA, Lund T (1996) Lipid biomarkers: linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea cod. Mar Ecol Prog Ser 131: 75–85

Stevens BG (1990) Temperature-dependent growth of juvenile red king crab (*Paralithodes camtschatica*) and its effects on size-at-age and subsequent recruitment in the eastern Bering Sea. Can J Fish Aquat Sci 47:1307–1317

Stevens BG, Lovrich GA (2014) King crabs of the world: species and distributions. In: Stevens BG (ed) King crabs of the world: biology and fisheries management. CRC Press, Boca Raton, FL, p 1–30

Stevens BG, Persselin S, Matweyou J (2008) Survival of blue king crab *Paralithodes platypus* Brandt, 1850, larvae in cultivation: effects of diet, temperature and rearing density. Aquacult Res 39:390–397

Stoner AW, Ottmar ML, Copeman LA (2010) Temperature effects on the molting, growth, and lipid composition of newly-settled red king crab. J Exp Mar Biol Ecol 393: 138–147

Stoner AW, Copeman LA, Ottmar ML (2013) Molting, growth, and energetics of newly-settled blue king crab: effects of temperature and comparisons with red king crab. J Exp Mar Biol Ecol 442:10–21

Tziouveli V, Smith GG (2012) A comparison of the fatty acid profiles of adult tissues, and newly hatched, fed and starved *Lysmata amboinensis* larvae. Aquacult Res 43: 577–587

Vinuesa JH, Varisco MA, Balzi P (2013) Feeding strategy of early juvenile stages of the southern king crab *Lithodes santolla* in the San Jorge Gulf, Argentina. Rev Biol Mar Oceanogr 48:353–363

Viso AC, Marty JC (1993) Fatty-acids from 28 marine microalgae. Phytochemistry 34:1521–1533

Wen XB, Chen LQ, Ku YM, Zhou KY (2006) Effect of feeding and lack of food on the growth, gross biochemical and fatty acid composition of juvenile crab, *Eriocheir sinensis.* Aquaculture 252:598–607

Woodby D, Carlile D, Siddeek S, Funk F, Clark JLH (2005) Commercial fisheries of Alaska. Alaska Department of Fish and Game Special Publication No. 05–09, Anchorage, AK

Wu XG, Zeng CS, Southgate PC (2014) Ontogenetic patterns of growth and lipid composition changes of blue swimmer crab larvae: insights into larval biology and lipid nutrition. Mar Freshw Res 65:228–243

Xu XL, Ji WJ, Castell JD, Odor RK (1994) Essential fatty-acid requirement of the Chinese prawn, *Penaeus chinensis.* Aquaculture 127:29–40

Zhou S, Shirley TC (1997) Distribution of red king crabs and Tanner crabs in the summer by habitat and depth in an Alaskan fjord. Investig Mar 25:59–67

Zhou SJ, Shirley TC, Kruse GH (1998) Feeding and growth of the red king crab *Paralithodes camtschaticus* under laboratory conditions. J Crustac Biol 18:337–345

Zimmerman AR, Canuel EA (2001) Bulk organic matter and lipid biomarker composition of Chesapeake Bay surficial sediments as indicators of environmental processes. Estuar Coast Shelf Sci 53:319–341

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