Deep-Sea Research II 135 (2017) 78–94

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Ontogenetic, spatial and temporal variation in trophic level and diet of Chukchi Sea fishes

Jennifer M. Marsh[a,*], Franz J. Mueter[a], Katrin Iken[b], Seth Danielson[b]

[a] University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Juneau Fisheries Center, 17101 Point Lena Loop Road, Juneau, AK 99801, USA
[b] University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Fairbanks, AK 99801, USA

ARTICLE INFO

Available online 22 July 2016

Keywords:
Chukchi Sea
Food webs
Stable isotope analysis
climate change
Boreogadus saida
fish community
diets
trophic levels

ABSTRACT

Climate warming and increasing development are expected to alter the ecosystem of the Chukchi Sea, including its fish communities. As a component of the Arctic Ecosystem Integrated Survey, we assessed the ontogenetic, spatial and temporal variability of the trophic level and diet of key fish species in the Chukchi Sea using N and C stable isotopes. During August and September of 2012 and 2013, 16 common fish species and two primary, invertebrate consumers were collected from surface, midwater and bottom trawls within the eastern Chukchi Sea. Linear mixed-effects models were used to detect possible variation in the relationship between body length and either δ^{13}C or δ^{15}N values among water masses and years for 13 fish species with an emphasis on Arctic cod (*Boreogadus saida*). We also examined the fish community isotopic niche space, trophic redundancy, and trophic separation within each water mass as measures of resiliency of the fish food web. Ontogenetic shifts in trophic level and diet were observed for most species and these changes tended to vary by water mass. As they increased in length, most fish species relied more on benthic prey with the exception of three forage fish species (walleye pollock, *Gadus chalcogrammus*, capelin, *Mallotus villosus*, and Pacific sandlance, *Ammodytes hexapterus*). Species that exhibited interannual differences in diet and trophic level were feeding at lower trophic levels and consumed a more pelagic diet in 2012 when zooplankton densities were higher. Fish communities occupied different isotopic niche spaces depending on water mass association. In more northerly Arctic waters, the fish community occupied the smallest isotopic niche space and relied heavily on a limited range of intermediate δ^{13}C prey, whereas in warmer, nutrient-rich Bering Chukchi Summer Water, pelagic prey was important. In the warmest, Pacific-derived coastal water, fish consumed both benthic and pelagic prey. Examining how spatial gradients in trophic position are linked to environmental drivers can provide insight into potential fish community shifts with a changing climate.

1. Introduction

Marine ecosystems can be defined and compared by their trophic structure (Lindeman, 1942), which may be altered through climate-driven changes in productivity (bottom-up processes), or through predator removals by fishing and alterations in predator range (top-down processes). For example, following a climate shift to a warm regime in the 1970s in the Gulf of Alaska, a community-wide trophic restructuring occurred. The system switched from an ecosystem dominated by benthic crustaceans and forage fish to one dominated by higher trophic level predatory groundfish (Anderson and Piatt, 1999), leading to an increase in trophic level (TL) of the fishery catches from the 1970s through the early 1990s (Urban and Vining, 2008). Conversely, in the North Atlantic, fishing pressure on predatory groundfish, combined with oceanographic changes, resulted in a switch from an ecosystem dominated by demersal fishes to one dominated by small pelagic fishes, benthic crustaceans and bivalves (Frank, 2005). Most likely, the effects of climate and fishing pressure worked synergistically to restructure that ecosystem (Kirby et al., 2009). Therefore, while it can be difficult to tease apart the effects of climate change and fisheries removals on ecosystem structure, the combined effects can be dramatic.

Commercial fishery removals are currently prohibited in the US Arctic, i.e., the eastern Chukchi and western Beaufort seas (NPFMC, 2009), a region impacted by extreme seasonality and pronounced climate change (ACIA, 2004). By 2100, air and sea temperatures in the Arctic are expected to rise an additional 5 °C and 1.5 °C, respectively, under moderate carbon emission scenarios (IPCC, 2013). Moreover, the annual average Arctic sea ice extent has shrunk by 3.5–4.1% per decade, with larger decreases of 9.4% per decade (1979–2012) occurring in the summer (IPCC, 2013). It has

* Corresponding author. Fax: +11 907 796 5447.
E-mail address: jmmarsh@alaska.edu (J.M. Marsh).

http://dx.doi.org/10.1016/j.dsr2.2016.07.010
0967-0645/

been suggested that the central Arctic Ocean will be seasonally ice-free as early as 2040 (Holland et al., 2006; Wang and Overland, 2012). With warming and a longer open-water season there is an increased interest in shipping, oil exploration and development/expansion of commercial fisheries. Until the fisheries ban is lifted and/or the Arctic Ocean is seasonally ice-free, the Arctic Ocean offers an opportunity to study effects of climate change with limited confounding from anthropogenic activities.

Future effects of continued climate warming and potential anthropogenic disturbances might have large impacts on the Chukchi Sea ecosystem. Warming waters and reduced extent of the Bering Sea cold-pool, a persistent pool of cold (<2 °C) bottom water formed during sea ice brine rejection that acts as a thermal barrier to the expansion of subarctic fishes northward (Mueter and Litzow, 2008), may facilitate earlier seasonal migrations (Moss et al., 2009) or the establishment of some subarctic fishes in the Arctic (Hollowed et al., 2013). These changes could alter Chukchi food web structure through changes in predation and competition for food resources. Also, earlier ice retreat and a prolonged open-water season could lead to earlier phytoplankton blooms and extended growing seasons (Kahru et al., 2010). Observed and future changes in phytoplankton bloom timing and composition (Li et al., 2009), along with changes in zooplankton composition, increases in abundance (Ershova et al., 2015) and grazing pressure (Lane et al., 2008), could possibly weaken the currently strong pelagic–benthic coupling. Currently, cold temperatures in the spring and summer limit zooplankton growth and reproduction; therefore, much of the primary production (ice algae and phytoplankton) is not heavily grazed and settles from the water column to support high benthic biomass (Coyle and Pinchuk, 2002; Questel et al., 2013). These effects will most likely vary spatially, as water mass structure has a strong influence on the community composition and food web structure of the biota (Eisner et al., 2012; Iken et al., 2010). Fishes provide important links between lower and upper trophic levels, as well as between benthic and pelagic communities. Therefore, changes in trophic structure experienced by the fish community may alter the efficiency of the food web with important consequences for upper trophic level species, including seabirds and mammals important to subsistence in coastal communities.

The pelagic and demersal fish biomass in the Chukchi Sea is generally low compared with invertebrate biomass (Stevenson and Lauth, 2012). In previous surveys, 59 demersal fish species in 17 families have been identified in the Chukchi Sea (Barber et al., 1997; Norcross et al., 2010, 2013a). However, only 4 families and 10 species comprise the majority of the demersal fish community (~90%): Gadidae (Arctic cod *Boreogadus saida,* saffron cod *Eleginus gracilis*), Cottidae (Hamecon *Artediellus scaber*, Arctic staghorn sculpin *Gymnocanthus tricuspis*, shorthorn sculpin *Myoxocephalus scorpius*), Pleuronectidae (Bering flounder *Hippoglossoides robustus,* yellowfin sole *Limanda aspera,* Alaska plaice *Pleuronectes quadrituberculatus*), and Zoarcidae (polar eelpout *Lycodes polaris*) (Barber et al., 1997; Norcross et al., 2013a). Even fewer species have been observed in the pelagic fish community with the dominant species being Pacific herring (*Clupea pallasii*), juvenile chum salmon (*Oncorhynchus keta*), juvenile Arctic cod (*B. saida*), capelin (*Mallotus villosus*) and Pacific sandlance (*Ammodytes hexapterus*) (Eisner et al., 2012). These species tend to be segregated into three groups: cold-adapted polar species, coastal species, and Pacific species (Barber et al., 1997; Norcross et al., 2010). Moreover, species richness declines from warmer sub-arctic waters to cooler Arctic waters in the northern Chukchi Sea (Mueter et al., 2013), as well as from nearshore to offshore (Barber et al., 1997; Piatt and Springer, 2003). In previous surveys of the Chukchi Sea, Arctic cod have consistently been one of the most dominant species, in terms of both biomass and abundance, in both pelagic and demersal trawls (Barber et al., 1997; Eisner et al., 2013; Norcross et al., 2010, 2013a). This species plays a crucial role in the ecosystem as important prey for many migrating seabirds (Matley et al., 2012) and marine mammals (Bluhm et al., 2008; Crawford et al., 2015; Loseto et al., 2009). Arctic cod are considered a key species linking upper and lower trophic levels in a relatively simple food web (Whitehouse et al., 2014).

To evaluate potential future changes in the fish community it is necessary to understand the diets of different species. Stable isotope analyses provide an alternative and complementary approach to the more traditional stomach content diet analyses. Two stable isotopes, ^{15}N and ^{13}C, are commonly used to characterize trophic status and dynamics. The ratio of heavy to light nitrogen relative to a standard ($\delta^{15}N$) is used to assess trophic level based on a distinct stepwise enrichment from prey to consumer (Minagawa and Wada, 1984; Post, 2002). In contrast, $\delta^{13}C$ is conserved throughout the food web with minimal enrichment between trophic levels (0–1‰) and can be used to track diet sources and general feeding habitats; e.g., phytoplankton tends to be more depleted in ^{13}C than benthic primary producers (France, 1995). Unlike stomach content analysis, stable isotope analysis integrates only food items assimilated by consumers, accurately representing a transfer of organic matter between trophic levels, and integrates diet over time-scales ranging from weeks to months, depending on the tissue analyzed (Miller, 2006).

Previous studies using C and N stable isotopes to examine the diets and trophic levels of fauna in the Chukchi Sea have primarily examined benthic organisms, including fishes, but have been limited by small samples sizes and/or spatial coverage (Feder et al., 2011; Iken et al., 2010; McTigue and Dunton, 2014). Studies of a few replicates (usually 1–9 specimens of each fish species collected per water mass) have found differences in fish trophic levels between water masses. Because trophic level (based on $\delta^{15}N$) often increases with body length (e.g., Jennings et al., 2002; Marsh et al., 2012) it is important to consider the trophic position of fish species throughout their life history. For example, the stable isotope signatures of different size classes of five common fish species within a limited region of the northeastern Chukchi Sea typically had higher $\delta^{15}N$ values in larger size classes of Bering flounder (*H. robustus*), Arctic cod, polar eelpout (*L. polaris*), Arctic staghorn sculpin (*G. tricuspis*) and stout eelblenny (*Anisarchus medius*) (Edenfield et al., 2011). Here we build on the previous work by conducting a spatially comprehensive stable isotope study.

As a component of the Arctic Ecosystem Integrated Survey, this project presents a unique opportunity to assess the ontogenetic, spatial and temporal variability of the trophic level and diets of key fish species in the eastern Chukchi Sea using C and N stable isotope data, complementing ongoing stomach content studies in the region. In addition, we use community level measures to quantify isotopic niche space, trophic redundancy and trophic separation within each water mass. Our specific objectives are to: (1) create isoscapes of C and N stable isotope ratios based on the primary consumer *Calanus* spp. to quantify and visualize spatial isotopic gradient at the base of the pelagic food web; (2) describe the ontogenetic diets and trophic level of common marine and anadromous fish species in the eastern Chukchi Sea; (3) assess spatial variability in the stable isotopic composition of the fish community by size class; and (4) assess the trophic role of a key species, Arctic cod, within the Chukchi Sea fish food web relative to water mass characteristics. We hypothesize that individual species have unique trophic levels (based on $\delta^{15}N$) that change with body length and that diet source (based on $\delta^{13}C$) changes with body length. We further hypothesize that the stable isotope composition of fishes varies spatially across the Chukchi Sea, reflecting different source waters and communities.