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Characterization of carbon and nitrogen stable isotope gradients in the northern Gulf of Alaska using terminal feed stage copepodite-V *Neocalanus cristatus*

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ABSTRACT

Individual terminal-feeding copepodite-V stage *Neocalanus cristatus* were collected systematically in the northern Gulf of Alaska (GOA) near 60°N from 1998 to 2004 from which the natural abundance of stable carbon and nitrogen isotopes was measured. The data confirmed the existence of an isotopic cross-shelf gradient such that values low in ^{13}C content are diagnostic of oceanic production from the GOA when measured in organisms taken from Prince William Sound (PWS). The mean $^{13}C/^{12}C$ cross-shelf gradient of 3–4 delta units was relatively strong, with generally good separation between GOA and Prince William Sound observations, whereas the mean $^{15}N/^{14}N$ gradient of ~2 delta units was relatively weak, with frequent overlap between GOA and PWS observations. There was a seasonal $^{15}N/^{14}N$ increase in the GOA. The $^{13}C/^{12}C$ values observed in PWS were more consistent over time than those observed in the GOA. Distinctively high $^{13}C/^{12}C$ values that were similar to those typical of PWS were observed at the continental slope during three of the Mays in the 1998–2004 period. The circulation pattern associated with mesoscale eddies, when they occurred just south of the sampling line based on satellite sea-surface height anomaly data, suggested that cross-shelf flow in the offshore direction drove high slope $^{13}C/^{12}C$ values. These observations led to positing that high $^{13}C/^{12}C$ values reflect coastal carbon isotope signatures and diatom blooms. Based on samples from May 1996, the three GOA *Neocalanus* congeners had concordant isotopic patterns with relatively small systematic species differences confirming that the isotopic patterns observed for *N. cristatus* apply to other zooplankton.

1. Introduction

The relative importance of alternate production sources used by pelagic food webs can be estimated from differences in natural stable isotope composition. Patterns of isotopic values measured in higher trophic levels (TLs) reflect concomitant patterns in the utilization of production sources given distinctive isotopic differences among sources (Gearing, 1988). Various factors can lead to isotopic differences, such as primary producer processes or food chain length. An example of the latter is that because of high trophic level, nitrogen delivered into freshwater by anadromous salmon is enriched in ^{15}N compared to background levels; this enables detecting salmon-derived nitrogen in freshwater food webs (e.g., Kline et al., 1990). Primary producer enzymatic systems typically discriminate in favor of ^{12}C over ^{13}C and ^{14}N over ^{15}N during uptake of dissolved inorganic carbon and nitrogen (other than nitrogen fixation). The resultant isotopic variation is propagated into food webs because of predictable isotopic relationships between consumer and diet (reviewed by Wada et al., 1991). Because a prerequisite for using stable isotope analysis (SIA) is to establish distinctive isotopic differences, there must thus be some consistency to the stable isotope 'signatures' from among the production sources defined for a given context. For example, the degree to which primary producers fractionate isotopes of C and N can be variable in space and time dictating the need for comprehensive sampling in order to characterize isotopic values of production sources with veracity.

The primary purpose for this study was to enable interpretation of juvenile salmon stable isotope data that were collected during 1998–2004 in the northern Gulf of Alaska (GOA) and Prince William Sound (PWS). The $^{13}C/^{12}C$ values of juvenile salmon and salmon marine survival rate were inversely correlated (Kline et al., 2008). It was thus necessary to validate the concept that low $^{13}C/^{12}C$ values were diagnostic of oceanic food subsidies as proposed by Kline (1999). This was done by systematically analyzing the stable isotope composition of individual terminal-feeding stage *Neocalanus cristatus*, a particle-feeding copepod commonly found in the study area, over space and time.

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2. Materials and methods

2.1. Rationale

Different approaches have been used to characterize isotopic values of low trophic level references used as production source proxies. One approach is to analyze bulk composite material retained on glass fiber filters from the contents of water sampling bottles, or from the material collected by plankton nets. Disadvantages of the bulk sample approach include the uncertain composition of the sample and that only one sample is generally obtained from one bottle (typically limited to a discrete depth) or net tow. Because there may be systematic differences in isotopic composition due to the various trophic positions of the organisms comprising bulk samples, sample-to-sample isotopic variation may reflect a sample's taxonomic nature (e.g., which kingdoms, phyla, etc., comprise the sample) and not the desired horizontal spatial and temporal variability of the food chain base.

An alternative approach to bulk sample analysis is single-species (or a single taxon of higher taxonomic level) SIA. Assuming that a single species (and, if possible, single life-stage) reflects a consistent trophic level, trophic isotope effects will have been minimized. Time integration is an important consideration when selecting a taxon for SIA as different taxa may reflect different temporal integrations. For example, Vander Zanden et al. (1997) used unionid mussels as their reference organism when estimating fish trophic levels using δ^{15}N values because they reflected relatively long period ($\geqslant$1 year) time-integrated consumption of primary producers. Shorter-term variation, such as seasonal isotopic shifts, can be measured by analyzing organisms with short generation times such as certain zooplankton. Taxonomic selection criteria should depend upon project goals as well as availability and practicality for sampling and isotopic analysis.

Performing SIA on individuals of a given species, rather than on composite samples of multiple individuals (e.g., pooling the individuals of a given species from a given net tow), allows one to assess population statistics and the detection of stable isotope modes in the population that might not otherwise have been observed (Kline, 1999). For example, there can be considerable physiological variation among individual copepods of a given species and stage (Båmstedt, 1988) that could contribute to isotopic variation that would otherwise not be detected. Each individual zooplankter forms a 'natural sampling unit' since each will have had a different temporal and spatial history. In the case of zooplankton, it is largely that of a passively moving particle driven by ocean physics as well as by specific life history pattern such as vertical migration and stage duration. Sampling one species thus also eliminates the potentially confounding effects of specific life history patterns.

The large (length ~9 mm) particle-feeding copepod *N. cristatus* at stage copepodite-V has been successfully used for single-taxon individual SIA in the northern GOA (Kline, 1999). This species comprises a significant proportion of the spring zooplankton in the study area (Coyle and Pinchuk, 2005). It is less synchronous compared to the other *Neocalanus* enabling collection in the GOA throughout the growing season. The time integration of a terminal-feeding copepodite-V stage *N. cristatus* is estimated to be on the order of one month.

N. cristatus was selected as the taxon for SIA for this study because individuals met minimal mass requirements, and because they were available in sufficient number to enable statistical analysis of the resultant data. Sample number of *N. cristatus* per net tow was previously a limitation (Kline, 1999) because 0.5-m diameter ring nets were used to sample terminal-feeding stages in PWS where they are less abundant compared to the GOA. As a result, it was necessary for Kline (1999) to pool data among several stations, limiting analysis to broad-scale comparisons of the GOA versus PWS. For this study, however, a large-volume sampling device enabled collecting sample sizes sufficient for comparisons among stations, among groups of stations, as well as GOA versus PWS.

To improve the context of using *N. cristatus* as the low trophic level reference for interpreting SIA of higher trophic levels, salmon in particular, the SIA of *N. cristatus* was compared to that of the other two *Neocalanus* species found in the GOA. This was done on samples from a single cruise in 1996, which was prior to the start of the systematic sampling that forms the bulk of this report. The sampling strategy employed during 1998–2004 was largely based upon these results.

2.2. Cruises

Sampling for the three *Neocalanus* congeners took place on R/V *Alpha Helix* cruise number HX192 in May 1996. The principal sampling of *N. cristatus* for this report took place on research cruises that were part of the Long Term Observational Program (LTOP), which was part of the Coastal Gulf of Alaska (CGOA) component of the Northeast Pacific Program (NEP) component of the US Global Ocean Ecosystem Dynamics (GLOBEC) program that took place during 1998–2004. See Batchelder et al. (2005) for an overview of the NEP-GLOBEC program. All but one LTOP cruise was done using the R/V *Alpha Helix* (Table 1). Two of the years during the CGOA-NEP study, 2001 and 2003, were designated as process study years for more intensive field sampling compared to other years. Connections with these process studies are referred to in Section 4. LTOP field sampling of *Neocalanus* for SIA took place in two phases. During phase I, 1998–2000, sampling for SIA took place during May. During phase II, sampling for SIA was done up to five times per year (Table 1).

HX192 was timed to catch the peak in occurrence of *Neocalanus* copepodite-V stages in PWS in May. *Neocalanus* were selected randomly for SIA from 10 MOCNESS tows made during HX192 (Table 1, Fig. 1). *Neocalanus plumchrus* were abundant at only four of these stations, whereas *N. cristatus* and *Neocalanus flemingeri* were abundant at all 10.

Sampling was done systematically on the sub-set of LTOP hydrographic stations, which were designated as core zooplankton stations (Weingartner et al., 2002; Coyle and Pinchuk, 2003, 2005). These core zooplankton stations consisted of 13 stations on the Seward Line, GAK1–GAK13, and five stations within PWS: MS2, HB2, KIP2, PWS1, and PWS2 (Coyle and Pinchuk, 2005; Table 1 and Fig. 1). Data from these stations were aggregated into one of four zones. GAK10–GAK13 were situated on the continental slope zone and designated as 'slope', whereas GAK5–GAK9, GAK1–GAK4, and those inside PWS were designated as 'outer shelf', 'inner shelf', and 'Sound', respectively (Table 1). CGOA NEP process studies were similarly divided into cross-shelf zones (e.g., Strom et al., 2006).

Other stations were sampled opportunistically as time allowed (Table 1). Hinchinbrook Entrance (HE) was sampled most frequently and was designated zone 'Entrance', whereas those on the Cape Cleare Southeast Line (CCSEs) were sampled only during 2001, depending on weather and available time. All core, HE, and CCSE stations were sampled for zooplankton with a MOCNESS. Other opportunistic stations not referred to above were sampled only one time each using a 1-m ring net of 0.5 mm mesh. CCSE and those stations sampled once were designated into zones according to cross-shelf position and depth (Table 1). The coarsest spatial scale consisted of placing all Gulf of Alaska stations into area category GOA, whereas all Prince William Sound stations