AN ABSTRACT OF THE DISSERTATION OF

Todd William Miller for the degree of Doctor of Philosophy in Fisheries Science presented on May 9, 2006.
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The Northern California Current (NCC) ecosystem exhibits extreme seasonal, interannual and interdecadal shifts in the abiotic environment and shifts in primary and higher production. This variability is also apparent in the spatial structure of the ecosystem with nearshore-shelf waters (<150 m isobath) being highly productive and having a different community structure relative to more offshore-slope (>150 m) waters. Very little is known of the trophic relationships between primary consumers and higher trophic levels within this system, and the potential influence of spatial gradients in productivity and community composition on trophic structure. This dissertation research covers several important aspects of trophic dynamics within the NCC ecosystem through the use of conventional dietary analysis and stable isotope analysis of multiple trophic levels. From June and August 2000 and 2002 cruises off the shelf-slope ecosystem from Northern California to central Oregon, I collected and analyzed the diets from 25 species of pelagic nekton (Chapter 2). Trophic groups were formed from agglomerative hierarchical cluster analysis of prey contribution to nekton diet, with cluster groups described by indicator species analysis. Seasonal, interannual and interdecadal comparisons in diet were examined for some nekton species. Results from general description of diets and cluster analysis showed clustering based primarily on prey of copepods, euphausiids, decapod larvae and larval-juvenile fishes, representing lower (copepods), middle (euphausiids and decapod larvae) and upper (larval-juvenile fishes) trophic groups, but that many species

exhibited omnivory by feeding on prey several levels down the food web. Results from carbon and nitrogen stable isotope analysis (Chapter 3) support the general trophic structure observed through dietary analysis; that the copepod-euphausiid-larval/juvenile fish structure in the diets were generally observed in relative trophic position using $\delta^{15}N$. Carbon stable isotopes displayed signatures more indicative of onshore-offshore distribution of species (Chapter 4) with nearshore species of nekton and zooplankton being enriched in ^{13}C relative to offshore. This provided an effective trophically-based delineation of the NCC pelagic food web. Although stable isotopes are effective tools for measuring relative trophic position and source production, the duration of time that stable isotopes are a measure of past trophic hsitory is not well known. To examine this, I conducted a laboratory-controlled experiment to examine the tissue-specific response of isotope $\delta^{15}N$ to changes in isotopic signature of diet in an adult marine fish (Pacific herring, *Clupea pallasi*)(Chapter 5). To test which animal tissue was the most accurate measure of isotope shift I examined multiple tissues (eye, heart, liver, blood, and white muscle) and the importance of growth and metabolism in this shift. This study showed that (*i*) isotopic response of individual tissues following an isotopic shift in diet varied in both rate of change and fractionation level, (*ii*) most of this isotopic shift is due to growth, and (*iii*) white muscle and liver tissue appeared the most responsive to isotopic shift in diet, reaching isotopic equilibrium with diet in a matter of months (not years). The culmination of this dissertation in the context of trophic controls on the NCC ecosystem, and how they are different from other EBC systems are discussed in Chapter 6.

TROPHIC DYNAMICS OF MARINE NEKTON AND ZOOPLANKTON WITHIN THE NORTHERN CALIFORNIA CURRENT PELAGIC ECOSYSTEM

by
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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Todd William Miller, Author

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Dr. Richard Brodeur assisted with data collection and analysis, provided laboratory space, supplies and logistical support for the research performed. Dr. Greg Rau provided additional data and use of his laboratory to run additional stable isotopes through his lab. Dr. Hiram Li provided extensive help with the manuscript and interpretation of results and provided laboratory space for research.

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CHAPTER 1

TROPHIC DYNAMICS OF THE NOTHERN CALIFORNIA CURRENT PELAGIC ECOSYSTEM

Todd W. Miller

INTRODUCTION

Understanding food web structure and dominant trophic pathways is essential to determining the factors which drive ecosystem diversity and stability (McCann 2000). The Northern California Current (NCC) exhibits extreme interannual and interdecadal fluctuations in ecosystem productivity (Corwith and Wheeler 2002) and community composition (Peterson et al. 2002, Brodeur et al. 2003, 2005) that have been linked to larger-scale atmospheric forcing and the strength and persistence of seasonal upwelling (Ware 1995, Mantua et al. 1997). However, the biotic interactions and trophic pathways of this ecosystem are not well understood. From sampling in the early 1980s, Brodeur and Pearcy (1992) provide the most comprehensive trophic analysis of the NCC pelagic ecosystem. However since that time the NCC has exhibited significant shifts in the abiotic environment (Peterson and Schwing 2003) and changes in nekton species composition (Brodeur et al. 2003). Knowledge of the primary trophic links within this system may better elucidate the response of this system to climate change and provide base information for ecosystem management and forecasting of future responses in fish production.

Few studies have directly examined entire food webs of large marine ecosystems (e.g. Brodeur and Pearcy 1992, Goldwasser and Roughgarden 1993, Garrison and Link 2000), with most using single species or narrow trophic groups to describe the system. Methods for analyzing the trophic relationships among species have historically relied on direct observation of feeding through stomach content analyses. More recently, analysis of stable isotopes have become an important ecological tool in elucidating relative trophic position (nitrogen stable isotopes) and tracing source production (carbon stable isotopes) of an organism's assimilated diet (Fry and Sherr 1984, Post 2002), which is based on the fundamental assumption that isotopes are temporally integrated within an organism from its food source (O'Reilly et al. 2002). However, few studies have examined the duration of isotopic integration in fish and none examined an adult marine pelagic species, which are a significant component of the marine pelagic food web.

Eastern boundary current (EBC) upwelling systems have been central to the discussion of what mechanisms regulate marine pelagic ecosystems (e.g. Cury et al. 2000, Ware and Thomson 2005). These systems are characterized as having high primary and secondary production, and a dominance of several baitfish species (anchovy and sardine), hake (Merlucciidae) and horse mackerel (*Trachurus* sp.)(Jarre-Teichmann 1998). Three leading concepts of how these systems are regulated are "top-down", "bottom-up" and "wasp-waist" control (Cury et al. 2003). Top-down and bottom-up controls are those biotic mechanisms that exert a trophic response from the bottom and top of the food web, respectively. Alternatively, wasp-waist control is based on the importance of one or several highly abundant mid-trophic species (usually small pelagic fishes such as sardine and anchovy) that exerts top-down control on zooplankton prey and early life history stages of adult predators, and bottom-up control on predators (Cury et al. 2003). As a condition of only a couple dominant mid-trophic species, wasp-waist control is typically associated with EBC upwelling regions and has been argued as a possible force in structuring the California, Benguela, Canary and Humbolt Current food webs (Cury et al. 2000).

In this Dissertation, I examined the dominant trophic relationships among pelagic nekton and zooplankton in the NCC ecosystem from field analysis of diets and stable isotopes, and examined the duration of isotopic integration in controlled laboratory experiments using adult Pacific herring (*Clupea pallasi*) as a model species. The objectives of this research were to determine the primary trophic links within this system (Chapters 2 and 3), and their spatial distribution (Chapters 2 and 4) that may contribute to top-down, bottom-up and/or wasp-waist control (Fig. 1.1).

Chapter 2 of this dissertation, entitled "Trophic Relationships of Marine Nekton within the Northern California Current", examines the spatial and temporal differences in diets among nekton species and multiple trophic levels using stomach content analysis. Stomach content analysis provides high quality information on the abundance of prey species or taxonomic groups consumed, however few studies have attempted this

approach in multiple species and trophic levels of a large marine ecosystem. This chapter provides the most recent and comprehensive trophic analysis of an eastern boundary upwelling zone since Brodeur and Pearcy (1992), and provides a view of the dominant trophic pathways between nekton and their prey during two years of very high productivity within the NCC ecosystem.

Chapter 3 entitled "Trophic Dynamics of Zooplankton and Nekton in the Northern California Current Ecosystem – an integrated approach using diet and stable isotope analyses" examined the trophic relationships between zooplankton and nekton using carbon and nitrogen stable isotopes, and compared these results with direct observations of stomach contents in Chapter 2. Stable isotopes are a useful tool in elucidating patterns in relative trophic position (Post 2002), sources of base production (Haines and Montague 1979, Fry and Sherr 1984) and patterns in organism movement (Fry 1981, Hesslein et al. 1991, Hansson et al. 1997), but they lack the descriptive details available through direct observation of feeding from stomach content analyses. The combination of these methods therefore provided a very comprehensive analysis of trophic interactions of nekton and zooplankton species. Results from this chapter confirmed the observations from Chapter 2 that many species from supposedly different trophic levels exhibited omnivory through consumption of euphausiids.

Chapter 4 entitled "Carbon Stable Isotopes Reveal Relative Contribution of Shelf-Slope Production to the Northern California Current Pelagic Community" examined the shelf-slope distribution of carbon stable isotopes relative to biotic and abiotic factors associated with nearshore upwelled and offshore-slope waters. Carbon stable isotopes have shown distinct differences between ecosystems with differences in primary production (Haines and Montague 1979), which is expressed at higher trophic levels (Perry et al. 1999). For coastal shelf-slope ecosystems where there exists a strong cross-shelf difference in primary production and associated $\delta^{13}C$ values (Schell et al. 1998), this difference may provide a reliable method for tracing nearshore-offshore advection of zooplankton and the transfer of nearshore versus offshore production to higher trophic levels. Results from

this chapter showed a gradual decrease in $\delta^{13}C$ from nearshore to offshore communities, with more nearshore-specific species being distinctly different in $\delta^{13}C$ from offshore-specific species; mid-shelf species expressed intermediate $\delta^{13}C$ values. The implication of this result is that $\delta^{13}C$ provides a spatial context to the NCC food web that can allow for subdivision of the ecosystem into shelf, shelf-slope, and slope species.

In Chapter 5 entitled "Tissue-specific Response of $\delta^{13}C$ in Adult Pacific Herring (*Clupea pallasi*) Following an Isotopic Shift in Diet", laboratory-controlled experiments were used to examine the time lag of $\delta^{15}N$ in various tissues of Pacific herring following a $\delta^{15}N$ shift in diet. Understanding the temporal integration of stable isotopes in fish is essential for providing a reasonable interpretation of field results. Prior to this study, no information was available on the temporal integration of stable isotopes in a marine pelagic species. Results from this study showed Pacific herring reach an isotopic ($\delta^{15}N$) equilibrium with their diet within months and that much of this shift was due to added tissue growth rather than tissue turnover. These results have a direct application to the interpretation of field results (Chapter 3).

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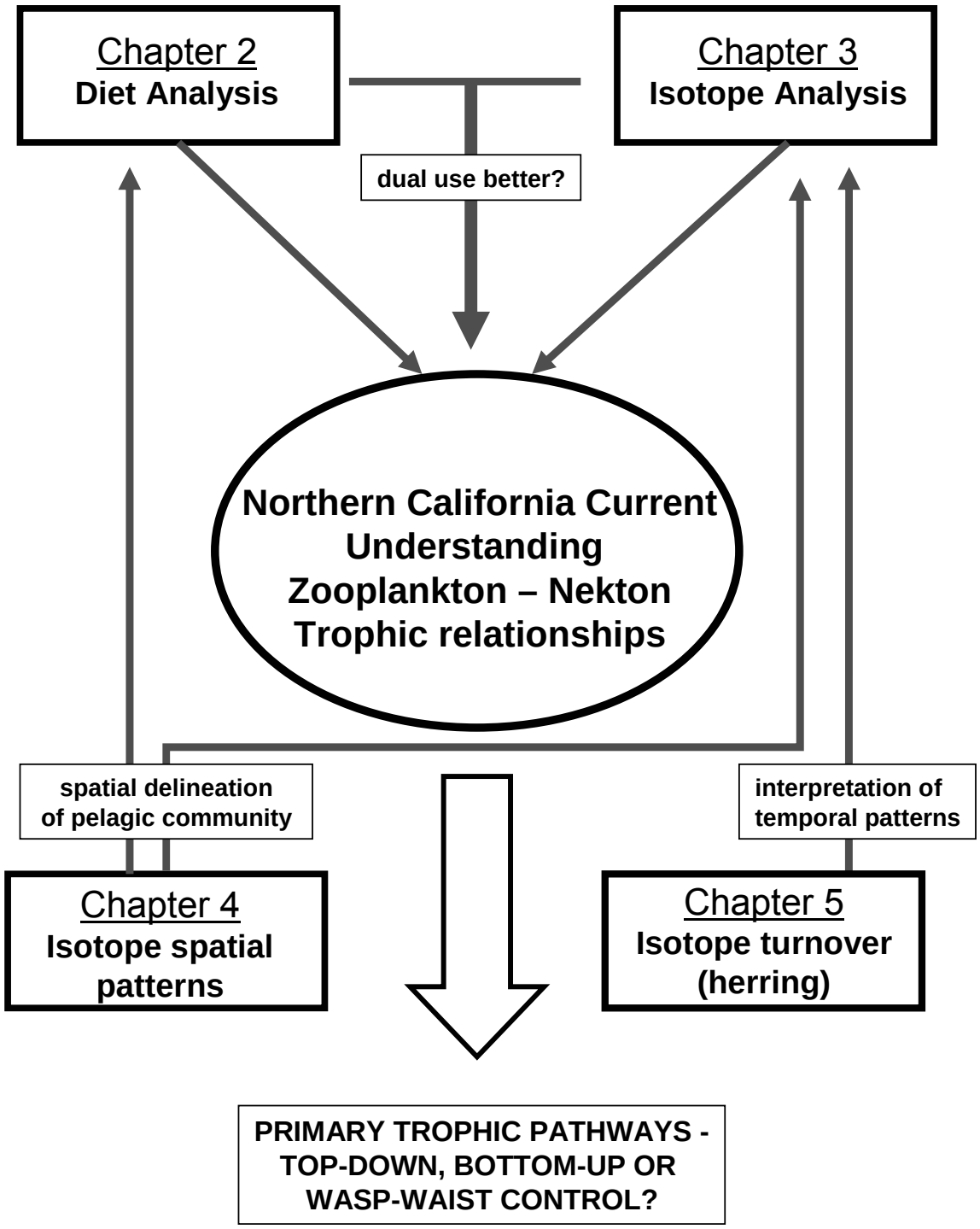

Figure 1.1. Interrelationships between dissertation Chapters 2-5.

CHAPTER 2

TROPHIC RELATIONSHIPS OF MARINE NEKTON WITHIN THE NORTHERN CALIFORNIA CURRENT ECOSYSTEM

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ABSTRACT

The Northern California Current (NCC) ecosystem exhibits extremes in seasonal, interannual and interdecadal abiotic factors and shifts in primary and higher production. However, very little is known of the trophic relationships between primary consumers and higher trophic levels within this eastern boundary upwelling zone. From June and August 2000 and 2002 cruises from Northern California to central Oregon, I collected and analyzed the diets from 25 species of pelagic nekton from the shelf-slope ecosystem. Trophic groups were formed from agglomerative hierarchical cluster analysis of prey contribution to nekton diet, with cluster groups described by indicator species analysis. Seasonal, interannual and interdecadal comparisons in diet were examined for some nekton species. Analysis of trophic groups relative to environmental parameters of sea surface temperature, salinity, chlorophyll-*a* , depth, distance from shore and latitude was performed using non-metric multidimensional scaling (NMS). Results from general description of diets and cluster analysis showed clustering of nekton based primarily on prey consumed of copepods, euphausiids, decapod larvae and larval-juvenile fishes representing low to upper trophic groups, respectively. However, certain prey were often found in multiple trophic groups, with euphausiids being the most widely consumed across trophic levels. Seasonal and interannual differences in diet varied considerably by species, with many differences in the percent wet weight contribution of prey to nekton diet due to shifts in euphausiids, fishes, copepods and decapod larvae. This high degree of variability in diet appears to override any interdecadal differences in diet between 2000 and 2002 and the 1980s. Results from cluster analysis and NMS of trophic groups during both years relative to environmental parameters showed trophic groups most associated with environmental parameters corresponding to differences between nearshore (shelf) and offshore (slope) waters. The general characterisitics of the NCC pelagic food web consists of a high degree of omnivory by consumption of euphausiids and larval juvenile fishes by upper trophic level species of blue sharks and adult sqalmonids. Mid-trophic wasp-waist species appear to also consume predominantly euphausiids and decapod larvae. The importance of euphausiids and other dominant zooplankton to the diets of nekton are discussed and compared to other ecosystems.

INTRODUCTION

Eastern boundary upwelling zones are highly productive and support major fisheries, yet these ecosystems also exhibit extreme fluctuations in primary production and higher trophic levels (Francis and Hare 1994, Ware 1995, Schwartzlose et al. 1999, Stapp et al. 1999, Chavez et al. 2003). Variation has been attributed to extremes in abiotic factors through relatively short term (interannual) El Niño and La Niña events (Pearcy and Schoener 1987), and through longer-term (decadal) environmental presses (Francis and Hare 1994, Mantua et al. 1997, Mantua and Hare 2002). This has led to considerable discussion regarding the movement of energy through large marine ecosystems and whether top-down or bottom-up processes prevail (Jackson et al. 2001). Despite this, few studies have attempted to provide a comprehensive view of trophic patterns within a system. Understanding trophic patterns and connectivity between species across multiple trophic groups is essential in understanding energy transfer within a system, and mechanisms behind ecosystem stability (Worm and Duffy 2003).

The northern California Current (NCC) system encompasses the northern region of the California Current production zone (Lat. 41° 46' - 49° 11' N) along the continental shelf and shelf break between northern California and Washington. This system is indicative of a major upwelling region, with sardine, anchovy, jack mackerel and squid and hake comprising the dominant nektonic species (Brodeur and Pearcy 1986, Brodeur et al. 2003). Between April-September strong and persistent coastal upwelling is the dominant hydrographic feature of the NCC, providing cool nutrient-rich water to surface waters across the shelf (Huyer 1983) allowing for high levels of primary production (Hood et al. 1991, Sackman et al. 2004). Interannual variation in coastal upwelling, particularly between El Niño and La Niña events, has been shown to greatly influence primary production (Corwith and Wheeler 2002) and higher trophic levels (Ainley et al. 1996, Peterson et al. 2002, McGowan et al. 2003). El Niño periods have been attributed to reduced growth and survival of salmonids (Johnson 1988, Beamish et al. 2004), seabird recruitment (Hodder and Graybill 1985) and dramatic changes in community composition of zooplankton (Peterson et al. 2002) and nekton (Brodeur et al. 1985, Emmett and

Brodeur 2000). Brodeur and Pearcy (1992) observed distinct trophic shifts in nekton diets during the 1982-83 El Niño event, indicating the inherent connection of trophic patterns and the abiotic environment. On an interdecadal scale, the California Current also experiences 30 yr+ "production regimes" that have been linked to salmon survival (Ware 1995, Mantua et al. 1997) and variations in NCC zooplankton biomass (Roemmich and McGowan 1995, Brodeur et al. 1996, McGowan et al. 1998). The response of this system appears related to variations in abiotic factors (McGowan et al. 1998) that influence nutrient supply and presumably energy transfer to higher trophic levels (Cole 2000, Koslow et al. 2002). However, few studies have examined the trophic relationships of nekton within this system or other eastern boundary upwelling regions. With the exception of diet analysis from a diverse assemblage of pelagic nekton by Brodeur et al. (1987) and Brodeur and Pearcy (1992) during the early 1980s off the Columbia River region, previous studies of the NCC have focused almost entirely on a small number of species (e.g., Ashton et al. 1985, Tanasichuk et al. 1991, Tanasichuk 1995, Buckley and Livingston 1997, Robinson 2000) or closely-related species (e.g. Peterson et al. 1982, Brodeur and Pearcy 1990, Brodeur 1992, Schabetsberger et al. 2003). Since that time the NCC system has exhibited shifts in the abiotic environment and biotic composition (Peterson and Schwing 2003) with a concomitant change in nekton species composition (Brodeur et al. 2003, Emmett and Brodeur 2000). Knowledge of feeding relationships among many species of nekton is essential for understanding the dynamics of competition, predation, and abiotic effects that may radiate through multiple trophic levels.

The purpose of this study was to provide a detailed description of the trophic relationships among the most abundant pelagic nekton species within the NCC system. Among the questions we asked were: i) what were the primary trophic relationships between dominant nekton and zooplankton in the NCC ecosystem; ii) how did trophic relationships change over time (seasonally, interannually and interdecal scales); and iii) how did spatial gradients in productivity across the shelf-slope ecosystem correspond to differences in fish diet?

METHODS

We examined the diets of dominant nekton species collected from June and August during 2000 and 2002 cruises along the continental shelf and shelf break of the NCC system. Multivariate methods of agglomerative hierarchical cluster analysis and non-metric multi dimensional scaling (NMS) were applied to examine trophic relationships and environmental patterns associated with nekton diets. We then compared our diet results to a similar study conducted by Brodeur et al. (1987) in the NCC during the early 1980's (1981-84); a period considered to be during a previous production regime (Peterson and Schwing 2003).

Field Collection

Nekton were collected for diet analysis from Northeast Pacific Global Ocean Ecosystems Dynamics (GLOBEC) cruises during 29 May-18 June and 29 July-12 August 2000, and 29 May-18 June and 31 July-19 August, 2002. Cruises are hereafter referred to as June and August as these months were when almost all the collections occurred. Sampling occurred along 9 transects across the shelf between Crescent City, California (Lat 41° 54.0') and Newport Oregon (Lat. 44° 39.0') (for station locations see Brodeur et al. (2004) and Reese and Brodeur (2006)), all occurring during daylight hours. At each station nekton were collected using a Nordic-264 rope trawl (30 m wide by 18 m deep) towed for 30 minutes. Up to 30 individuals per species were collected per tow for diet analysis. Upon collection, nekton were immediately frozen on ship (-20ºC) and later taken to the laboratory for processing. At each sample location, environmental data of sea surface (3m) temperature, salinity, and chlorophyll-*a* (chl-*a*) were measured.

Laboratory

Laboratory processing of nekton involved measurement of individuals and extraction of stomachs for diet analysis. Lengths of fish were measured (±1.0 mm) using either fork length (FL) or standard length (SL). Market squid (*Loligo opalescens*) were measured using dorsal mantle length (DML). Stomachs were extracted and immediately placed in 10% buffered formalin for 10 d, then rinsed with tap water and transferred to 70%

ethanol. Diet analysis was performed by assessing fullness, digestive condition, and identification and quantification of prey taxa in each stomach. Fullness was assessed by applying a scale of 0-5, with 0 being empty, 4 full, and 5 distended. Digestive condition of individual prey was assessed using a 0-4 scale, with 0 being unrecognizable and 4 being fresh. Prey taxa were identified to lowest possible taxon, enumerated, and weighed (±0.0001g). In some instances, individual prey were too numerous to enumerate, therefore individual weights were obtained by obtaining the damp weight of a known number of animals and regressing this number to the total weight of the prey. For Pacific sardine, diets comprised large amounts of phytoplankton mixed with small zooplankton and euphausiid eggs, requiring a subsampling method for diet analysis. A detailed description of this procedure is provided in Emmett et al. (2005). Size-specific age classes were assigned to Chinook and coho salmon following Brodeur et al. (2004), with Chinook divided into subyearlings, yearlings and adults, and coho were separated into yearlings and adults.

Data Analysis

Trophic Relationships

Trophic relationships of nekton were examined using Agglomerative Hierarchical Cluster Analysis (AHCA) to form cluster dendrograms from a simple predator (row) x prey (column) matrix, using the percent damp weight contribution of prey to predator diets. For AHCA we used the Sørensen (Bray-Curtis) distance measure and flexible beta linkage method, with the flexible beta value set at -0.25. Cluster groups from dendrograms were established by choosing a cutoff level with biological meaning while maintaining a reasonable level (at least 50%) of information explained in the cluster dendrogram. The significance of cluster groups was examined using a multi-response permutation procedure (MRPP), which tests for the null hypothesis of no difference between groups. MRPP gauges within and between group differences using an A-statistic that ranges between 0 and 1, with 1 being 100% agreement within a group and 0 is no agreement. We then applied indicator species analysis (ISA, Dufrêne and Legendre 1997) to describe prey species that are indicative of each group from cluster analysis. Indicator

species analysis applies a Monte Carlo test using permutations of the data to assign the significance of indicator prey to a particular group; we applied 1000 permutations to the data. Prior to non-parametric analyses of diets, certain modifications to the data were performed. Nekton species that occurred in <5% of the tows within a cruise were excluded from analyses (these species were retained in the general description of diets). This level of exclusion was somewhat arbitrary, however exclusion of nekton species collected between 5-10% would have removed many species from analyses, and for many species the diet did not change markedly with increasing tows added. Prey taxa modifications involved removal and/or clumping of certain groups. Unidentified crustaceans, fish tissue and other material were removed due to their ubiquitous nature across all diets. Individual prey species of larval-juvenile fishes, hyperiid amphipods, brachyuran and decapod larvae, and adult fishes were combined into their respective higher taxonomic categories and life history stages. This was required to retain important species groups for multivariate analyses. Adjustments for all data involved the removal of rare prey species that were only present in $\leq$10% of the nekton diets (rows) in the main matrix and general relativization by prey species (columns). Removal of rarer species reduced noise in the data and allowed for comparisons based on important prey between nekton predators, whereas general relativization of prey species reduces total column coefficient of variation reducing the chance of clustering of predators with high values (McCune et al. 2002).

Trophic relationships were also analyzed by calculating the degree of diet similarity between nekton species pairs by using Schoener's similarity index (PSI; Schoener 1974), modified as a percent similarity between the diets of paired nekton (Brodeur and Pearcy 1992):

$$\mathrm{PSI} = \left(1 - 0.5\sum_{i=1}^{n}\left|p_{ik} - p_{jk}\right|\right)\times 100 \qquad (1)$$

Where *p* is the proportion of biomass (wet weight) of *k*th prey species consumed by predator species *j* and *k*. Diet overlap values ≥ 60% were considered biologically significant (Wallace and Ramsay 1983).

Trophic Group Association with Environmental Parameters

To explore potential patterns in nekton diets that may be associated with environmental parameters we used AHCA and non-metric multidimensional scaling (NMS; Kruskal 1964) to a trophic matrix that combined the predator and sample station as rows and prey as columns. The rows represented a particular predator species and diet analyzed from a specific station, with columns representing the average percent wet weight composition of prey consumed from a predator at that particular station. Cluster dendrograms were created using AHCA, with groups formed by choosing a cutoff level of <50% while still maintaining a moderate level of within-group agreement (A-statistic >0.1; McCune et al. 2002) using MRPP. Groups were then described in terms of prey by using ISA; a Monte Carlo test using 1000 permutations of the data was performed to assign significance of indicator prey to a particular group. To examine spatial properties associated with groups and prey consumed we used NMS (Sørensen distance measure, 3 axis, 100 maximum number of iterations) to form joint plots of the second environmental matrix of predator-station (rows) and environmental parameters (columns). This allowed for the visual examination of any correlation of environmental parameters to structure in the diet data. Environmental parameters examined were 3 m depth temperature, salinity and chlorophyll-*a* (chl-*a*), station distance offshore, time of collection, and bottom depth at location of collection. Environmental parameters expressing an R^2 of $\geq$0.10 to trophic relationships were displayed on joint plots. Stress values of the NMS ordination were generated as a measure of goodness of fit, in which values <20 are considered to have interpretable results (McCune et al. 2002).

Temporal – Seasonal and Interannual Comparisons

Diets from selected species were compared with respect to seasonal (June and August) and interannual differences. Comparisons were made by visual assessment of the percent

damp weight contribution to diet. Seasonal comparisons of nekton were limited to species that occurred in >5% of the total number of hauls within a cruise. This resulted in five species between June and August for 2000 (surf smelt, yearling and adult Chinook salmon, juvenile coho salmon and steelhead trout) and six (yearling and adult Chinook salmon, juvenile coho salmon, Pacific saury, Pacific herring and market squid) for 2002. Interannual comparisons of diets were limited using the same procedure for seasonal comparisons with the condition that a species had to be present in both June and August cruises from a particular year to remove seasonal bias in the data. This left only yearling and adult Chinook and juvenile coho salmon for between-year comparisons.

Interdecadal Comparison

Comparison of diets with those examined by Brodeur and Pearcy (1992) for 1981 to 1984 was performed using a main matrix of predator/cruise (rows) x prey species (columns) using NMS. Joint plots showing the distribution of a predator during a particular cruise with respect to prey (joints) was formed by overlaying a second matrix of predator/cruise (rows) x prey species (columns) primary matrix. Prey species expressing an R^2 of $\geq$0.10 were displayed on joint plots. Analysis was limited to August-September collections of juvenile coho and Chinook salmon, adult Chinook salmon and jack mackerel due to limitations in the availability of the same species in abundance every year. Modifications to the data involved removal of rare species ($\leq$10% frequency of occurrence in rows) and general relativization. This analysis assumes that potential differences in time of sampling and location between the two research projects has a minimal effect on diet analysis results.

RESULTS

From the June and August 2000 and 2002 cruises, a total of 3177 stomachs from 25 species of marine nekton were analyzed for diet analysis (Tables 2.1-2.4). Overall, mean stomach fullness for fish analyzed was 2.7, corresponding to stomachs that were approximately 50% full; mean digestive condition factor was 1.9, indicating that most prey were identified to genera or family level (Tables 2.1-2.4). Salmonids (Chinook,

coho, and chum salmon and steelhead trout), Clupeiformes (sardine, anchovy and herring), and Scorpaeniformes (juvenile rockfish and hexagrammids) typically had the highest fullness factors (mean 3.1, 3.4 and 2.6, respectively), whereas cephalopods (market squid) and elasmobranchs (blue shark and spiny dogfish) had relatively empty stomachs (mean 1.4 and 0.6, respectively) (Tables 2.1-2.4). Diet descriptions of all species are provided in Fig. 2.1-2.4 and Appendix A. Detailed dietary analysis of juvenile and adult salmon are provided in Baldwin et al. (in–prep.).

Trophic Relationships

Cluster analysis of predator diets (% wet weight) and application of MRPP and ISA resulted in trophically-based cluster groups within each cruise, however patterns in group membership shifted over time. For June 2000, three significant (A=0.17, p=0.005) groups were observed at the cutoff level of 25% information remaining (Fig. 2.1). One group was excluded from MRPP and ISA because it only contained one species (group A, Fig. 2.1, pelagic juvenile lingcod). This group contained the lowest trophic level based on its diet, consisting primarily of euphausiid furcilia (~60% wet weight of diet) and copepods (~30%, Fig. 2.1, Appendix A). A mid-trophic group (group B, Table 2.5, Fig. 2.1) containing juvenile sablefish, Pacific herring, and whitebait smelt had three indicator species with only euphausiids (unidentified to species) being significant (ISA p=0.004); the remaining two species were euphausiid furcilia and hyperiid amphipods, both non-significant (p>0.5 for both). A mid-upper trophic group (group C, Table 2.5, Fig. 2.1) contained surf smelt and market squid, which had the most indicator species (n=5 out of 11) and the highest number (n=3) that were significant. Significant indicator species were brachyuran larvae (p=0.03), *Cancer* spp. larvae (p=0.05) and euphausiid eggs (p=0.05), with larval and juvenile decapods being moderately (p=0.08) and highly (p=0.56) non-significant. The highest trophic group (group D, Table 2.5, Fig. 2.1), consisting of adult and yearling Chinook, juvenile steelhead trout and yearling coho salmon, had three indicator species with only one, *Euphausia pacifica*, being significant (p=0.01). The other two indicator species were larval-juvenile Osteichthyes (p=0.11) and the euphausiid *Thysanoessa spinifera* (p=0.88).

Table 2.1. June 2000. Summary statistics of nekton for diet (stomach content) analysis. Stomach fullness based on a 0 (empty) to 5 (distended) stomach, and digestion based on 0 (well digested) to 4 (fresh).

June 2000 Cruise		F.O.	Fullness		Digestion		Length (mm)	
Taxa	N	(%)	Mean	S.D.	Mean	S.D.	Mean	S.D.
Mollusca								
Market Squid (*Loligo opalescens*)	38	4.8	0.8	1.3	0.4	1.0	72	17
Osteichthyes								
Clupeiformes								
Pacific Herring (*Clupea pallasi*)	134	8.3	3.6	1.4	2.5	1.3	146	11
Pacific Sardine (*Sardinops sagax*)	7	2.4	1.2	1.9	1.5	0.8	244	10
Osmeriformes								
Surf Smelt (*Hypomesus pretiosus*)	163	6.0	2.3	1.4	2.5	0.8	144	7
Whitebait Smelt (*Allosmerus elongatus*)	38	4.8	3.6	1.0	2.3	0.9	89	10
Salmoniformes								
Chinook Salmon (subyearling) (*Oncorhynchus tshawytscha*)	1	1.2	3.0		3.0		121	
Chinook Salmon (yearling) (*Oncorhynchus tshawytscha*)	26	8.3	3.5	1.5	2.5	1.2	224	40
Chinook Salmon (adult) (*Oncorhynchus tshawytscha*)	19	14.3	3.2	1.5	2.9	1.0	334	34
Coho Salmon (yearling) (*Oncorhynchus kisutch*)	32	16.7	4.4	0.9	3.0	1.1	171	34
Coho Salmon (adult) (*Oncorhynchus kisutch*)	1	1.2	4.0		4.0		580	
Cutthroat Trout (adult) (*Oncorhynchus clarki clarki*)	1	1.2	5.0		0.0		186	
Steelhead Trout (juvenile) (*Oncorhynchus mykiss*)	21	8.3	4.4	1.3	1.7	1.5	244	29
Scorpaeniformes								
Sablefish (juvenile) (*Anaplopoma fimbria*)	2	2.4	3.7	0.6	1.7	0.6	68	14
Lingcod (juvenile) (*Ophiodon elongatus*)	10	4.8	3.8	0.6	2.7	0.8	74	4
Darkblotched Rockfish (juvenile) (*Sebastes crameri*)	7	1.2	4.0	1.1	0.5	0.5	47	4
Yellowtail Rockfish (juvenile) (*Sebastes flavidus*)	26	2.4	2.2	1.5	0.1	0.4	49	4
Rockfish (juvenile) (*Sebastes* sp.)	4	1.2	4.0		1.0		48	2
Perciformes								
Jack Mackerel (*Trachurus symmetricus*)	11	1.2	3.4	1.2	2.1	0.9		
Total	541							

Table 2.2. August 2000. Summary statistics of nekton for diet (stomach content) analysis. Stomach fullness based on a 0 (empty) to 5 (distended) stomach, and digestion based on 0 (well digested) to 4 (fresh).

August 2000 Cruise		F.O.	Fullness		Digestion		Length (mm)	
Taxa	N	(%)	Mean	S.D.	Mean	S.D.	Mean	S.D.
Chondrichthyes								
Blue Shark (*Prionace glauca*)	9	6.3	0.6	0.6	0.6	0.8	1331	136
Clupeiformes								
Northern Anchovy (*Engraulis mordax*)	4	2.5	3.2	1.8	0.8	0.4	152	6
Pacific Sardine (*Sardinops sagax*)	153	13.9	2.9	1.6	2.5	1.4	220	28
Osmeriformes								
Surf Smelt (*Hypomesus pretiosus*)	94	5.1	1.8	1.2	2.0	1.1	144	7
Whitebait Smelt (*Allosmerus elongatus*)	51	3.8	3.8	1.3	3.1	1.1	109	8
Salmoniformes								
Chinook Salmon (subyearling) (*Oncorhynchus tshawytscha*)	55	3.8	2.4	1.4	1.7	0.9	137	14
Chinook Salmon (yearling) (*O. tshawytscha*)	74	21.5	3.5	1.3	2.3	0.8	226	26
Chinook Salmon (adult) (*O. tshawytscha*)	13	10.1	2.1	1.6	2.1	0.7	443	55
Coho Salmon (yearling) (*O. kisutch*)	52	21.5	3.1	1.5	2.5	0.8	316	57
Coho Salmon (adult) (*O. kisutch*)	12	7.6	3.4	1.8	2.6	1.2	595	71
Cutthroat Trout (adult) (*O. clarki clarki*)	3	2.5	1.9	0.4	2.1	0.4	334	19
Steelhead Trout (juvenile) (*O. mykiss*)	34	16.5	3.8	1.3	2.7	0.8	308	29
Steelhead Trout (adult) (*O. mykiss*)	1	1.3	1.0		3.0		430	
Beloniformes								
Pacific Saury (*Cololabis saira*)	40	5.1	1.4	1.2	0.8	1.0	157	22
Scorpaeniformes								
Sablefish (*Anaplopoma fimbria*)	4	2.5	4.3	1.3	2.2	1.4	202	27
Perciformes								
Jack Mackerel (*Trachurus symmetricus*)	75	11.4	3.2	1.7	2.2	1.2	497	74
Pacific Mackerel (*Scomber japonicus*)	19	1.3	1.5	1.8	0.4	0.5	325	24
Total	693							

Table 2.3. June 2002. Summary statistics of nekton for diet (stomach content) analysis. Stomach fullness based on a 0 (empty) to 5 (distended) stomach, and digestion based on 0 (well digested) to 4 (fresh).

June 2002 Cruise		F.O.	Fullness		Digestion		Length (mm)	
Taxa	**N**	**(%)**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**
Mollusca								
Market Squid (*Loligo opalescens*)	88	5.8	2.5	1.8	0.7	1.0	96	31
Chondrichthyes								
Blue Shark (*Prionace glauca*)	4	1.9	2.6	1.1	1.6	0.8	1447	315
Spiny Dogfish (*Squalus acanthias*)	65	5.8	0.3	0.6	0.1	0.2	372	57
Clupeiformes								
Northern Anchovy (*Engraulis mordax*)	32	2.9	1.1	0.4	0.6	0.8	122	4
Pacific Herring (*Clupea pallasi*)	103	6.7	2.3	1.4	1.4	1.1	172	24
Pacific Sardine (*Sardinops sagax*)	49	6.7	2.9	1.9	2.6	1.0	232	37
Osmeriformes								
Surf Smelt (*Hypomesus pretiosus*)	46	2.9	3.9	0.9	2.3	0.7	153	14
Whitebait Smelt (*Allosmerus elongatus*)	60	1.9	1.5	1.7	1.1	1.3	107	5
Salmoniformes								
Chinook Salmon (subyearling) (*Oncorhynchus tshawytscha*)	1	0.9	5.0		2.0		129	
Chinook Salmon (yearling) (*O. tshawytscha*)	68	25.0	3.0	1.6	2.3	0.9	220	30
Chinook Salmon (adult) (*O. tshawytscha*)	68	27.9	2.9	1.6	2.7	0.8	412	126
Coho Salmon (yearling) (*O. kisutch*)	119	25.0	3.8	1.2	2.6	0.9	182	38
Coho Salmon (adult) (*O. kisutch*)	11	8.7	4.0	1.0	3.7	0.6	514	56
Chum Salmon (juvenile) (*O. keta*)	147	10.6	2.7	1.5	2.4	0.9	113	11
Steelhead Trout (juvenile) (*O. mykiss*)	9	5.8	4.5	1.1	2.7	0.9	230	37
Gadiformes								
Pacific Hake (*Merluccius productus*)	29	1.9	2.1	1.5	2.2	1.4	66	94
Beloniformes								
Pacific Saury (*Cololabis saira*)	26	5.8	1.6	2.1	0.8	1.3	276	15

(CONTINUED)

Table 2.3 (Continued). June 2002. Summary statistics of nekton for diet (stomach content) analysis. Stomach fullness based on a 0 (empty) to 5 (distended) stomach, and digestion based on 0 (well digested) to 4 (fresh).

June 2002 Cruise		F.O.	Fullness		Digestion		Length (mm)	
Taxa	**N**	**(%)**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**
Scorpaeniformes								
Bank Rockfish (juvenile) (*Sebastes rufus*)	9	1.0	2.3	0.5	1.1	1.2	31	3
Canary Rockfish (juvenile) (*Sebastes pinniger*)	16	2.9	3.2	1.3	1.0	0.8	27	3
Darkblotched Rockfish (juvenile) (*Sebastes crameri*)	11	2.9	3.3	1.0	1.6	0.7	29	2
Rockfish (juvenile) (*Sebastes* sp.)	19	2.9	3.6	1.1	1.5	1.0	37	7
Widow Rockfish (juvenile) (*Sebastes entomelas*)	41	4.8	4.3	1.0	2.8	0.8	53	4
Lingcod (juvenile) (*Ophiodon elongatus*)	1	1.0	5.0		3.0		64	
Perciformes								
Jack Mackerel (*Trachurus symmetricus*)	82	7.7	2.3	1.8	1.3	1.0	501	96
Pacific Sandlance (juvenile) (*Ammodytes hexapterus*)	73	5.8	3.2	1.4	2.5	1.4	57	5
Total	1177							

Table 2.4. August 2002. Summary statistics of nekton for diet (stomach content) analysis. Stomach fullness based on a 0 (empty) to 5 (distended) stomach, and digestion based on 0 (well digested) to 4 (fresh).

August 2002 Cruise		**F.O.**	**Fullness**		**Digestion**		**Length (mm)**	
Taxa	**N**	**(%)**	**Mean**	**S.D.**	**Mean**	**S.D.**	**Mean**	**S.D.**
Market Squid (*Loligo opalescens*)	90	5.9	1.0	1.3	0.2	0.6	71	18
Chondrichthyes								
Blue Shark (*Prionace glauca*)	9	4.0	1.0	1.0	0.6	0.8	1678	198
Clupeiformes								
Northern Anchovy (*Engraulis mordax*)	63	6.9	2.9	1.7	1.9	1.0	150	10
Pacific Herring (*Clupea pallasi*)	145	14.9	3.6	1.6	2.5	1.1	164	18
Pacific Sardine (*Sardinops sagax*)	49	4.0	3.5	1.4	3.4	0.7	234	21
Osmeriformes								
Surf Smelt (*Hypomesus pretiosus*)	59	2.0	1.7	1.5	1.0	1	168	12
Whitebait Smelt (*Allosmerus elongatus*)	41	2.0	1.8	1.9	1.6	1.6	117	7
Salmoniformes								
Chinook Salmon (subyearling) (*Oncorhynchus tshawytscha*)	9	3.0	3.3	1.0	2.6	0.7	122	19
Chinook Salmon (yearling) (*O. tshawytscha*)	28	15.8	3.2	1.9	2.7	0.9	288	30
Chinook Salmon (adult) (*O. tshawytscha*)	32	16.8	3.0	1.8	2.5	0.8	410	38
Coho Salmon (yearling) (*O. kisutch*)	32	16.8	3.7	1.3	2.6	0.8	304	69
Chum Salmon (juvenile) (*O. keta*)	1	1.0	0.0		0.0		182	
Cutthroat Trout (adult) (*O. clarki clarki*)	7	5.9	3.9	1.3	2.5	0.6	321	28
Steelhead Trout (juvenile) (*O. mykiss*)	6	5.0	3.6	1.5	2.3	0.8	323	19
Gadiformes								
Pacific Hake (*Merluccius productus*)	43	2.0	2.6	1.6	2.6	1.1	377	21
Beloniformes								
Pacific Saury (*Cololabis saira*)	114	5.9	2.9	1.3	1.3	1.3	199	43
Scorpaeniformes & Perciformes								
Sablefish (*Anaplopoma fimbria*)	15	5.0	4.5	1.0	1.9	1.1	181	9
Jack Mackerel (*Trachurus symmetricus*)	160	15.8	2.3	2.0	1.1	1.1	508	33
Total	903							

August 2000 fish displayed three significant groups (A = 0.29, p = 0.003) at the cutoff level of 27% information remaining (Fig. 2.2). One group (group A, Fig. 2.2) consisted of juvenile steelhead trout, jack mackerel, Pacific sardine, Pacific saury, and Pacific mackerel and had listed two indicator prey species, *Euphausia pacifica* and euphausiids, both of which were non-significant (p=0.09 and 0.08, respectively, Table 2.5). A middle group (group B, Fig. 2.2) consisted of adult and yearling Chinook salmon, yearling Coho salmon, and surf smelt. This group had the highest number of indicator species (n=7), however only one species, *Cancer* spp. larvae, was significant (p=0.008), with larval-juvenile Osteichthyes being moderately non-significant (p=0.07). The highest trophic group (group C, Fig. 2.2) contained adult coho salmon and blue shark, which had adult Osteichthyes as the only indicator species (significant, p=0.02).

June 2002 fish consisted of four significant groups (MRPP A = 0.10, p = 0.0002) at the 37% information remaining cutoff level (Fig. 2.3). The lowest trophic group (group A, Fig. 2.3) consisted of pelagic juvenile widow rockfish and adult Pacific sardine, with significant indicator species of euphausiid eggs and copepods (p=0.01 for both) and euphausiid furcilia (p=0.05)(Table 2.6). A mid-lower trophic group (group B, Fig. 2.3), containing juvenile Pacific sand lance, Pacific herring, and juvenile steelhead, had the highest overall number of indicator species (n = 5), with only one being significant (euphausiid *T. spinifera*, p = 0.009). Market squid (group C, Fig. 2.3) were placed within its own group and had a diet consisting primarily of decapod larvae and brachyuran larvae and juveniles, and crustacean material. A mid-upper trophic group (group D, Fig. 2.3) containing Pacific saury, juvenile coho and chum salmon, and yearling Chinook salmon, listed four indicator species, all of which were non-significant. The highest trophic group (group E, Fig. 2.3) contained Pacific hake, adult Chinook salmon, spiny dogfish and jack mackerel, with only one significant indicator species of larval-juvenile Osteichthyes (p=0.02); fish eggs were listed as the only other indicator species for this group (p=0.12).

Table 2.5. June and August 2000 summary of results from Indicator Species Analysis (ISA) of cluster groups based on agglomerative hierarchical cluster analysis of nekton diets. Life history stages of nekton and prey are in parentheses and represent: egg (e), megalopa larvae (m), larva (l), juvenile (j), furcilia (f), yearling (y) and adult (a); nekton and prey with no indication of life history stage are adult.

Cruise Period Nekton Species	Cluster Group	Indicator Prey Species	Indicator Value	p-value
June 2000				
Chinook salmon (y)	D	Osteichthyes (j)	71.6	0.119
Coho salmon (y)	D	*Thysanoessa spinifera*	34.5	0.888
Steelhead trout (j)	D	*Euphausia pacifia*	81.3	0.016
Chinook salmon (a)	D			
Market squid	C	Brachyura (l)	98.8	0.035
Surf smelt	C	*Cancer* spp. (l)	98.8	0.054
		Copepoda	43.1	0.056
		Decapoda (l, j)	73.1	0.079
		Euphausiidae (e)	90.8	0.049
Whitebait smelt	B	Euphausiidae (f)	25.0	0.65
Pacific herring	B	Euphausiidae	87.4	0.004
Sablefish (j)	B	Hyperiidea	32.2	0.986
Lingcod (j)	A	-		
August 2000				
Blue shark	C	Osteichthyes (a)	95.2	0.026
Coho salmon (a)	C			
Surf smelt	B	Brachyura (l)	49.9	0.169
Chinook salmon (y)	B	Copepoda	90.7	0.008
Coho salmon (y)	B	Osteichthyes (j)	19.6	0.899
Chinook salmon (a)	B	Euphausiidae (f)	45.9	0.076
		Hyperiidea	59.7	0.382
		Thysanoessa spinifera	54.4	0.228
Pacific mackerel	A	*Euphausia pacifica*	75.0	0.091
Pacific saury	A	Euphausiidae	71.4	0.083
Pacific sardine	A			
Jack mackerel	A			
Steelhead trout (j)	A			

Cluster analysis of August 2002 fish resulted in only three cluster groups at the cutoff level of 27% information remaining (Fig. 2.4). Only two of the three groups could be compared using MRPP and ISA because one group contained only one species. The single-species group contained blue shark (group C, Fig. 2.4), which generally consumed adult fish and cephalopods (Fig. 2.4, Appendix A). No difference was observed between the two multi-species groups (MRPP A=0.03, p=0.7). The first group contained yearling and adult Chinook salmon, juvenile coho salmon, juvenile sablefish, northern anchovy, jack mackerel and Pacific herring (group A, Fig. 2.4). This group listed two significant indicator species (Table 2.6), adult euphausiids and *T. spinifera* (p=0.03 for both), and two moderately-nonsignificant taxa including *E. pacifica* (p=0.08) and larval-juvenile Osteichthyes (p=0.06). The other multi-species group (group B, Fig. 2.4) contained only market squid and Pacific saury, with one significant (p=0.03) indicator species for gelatinous material.

Percent similarity of diets between nekton species varied by cruise (Tables 2.7-2.10). During June 2000 (Table 2.7), highest overlap values were between whitebait smelt and Pacific herring (79.2%), steelhead trout and adult Chinook (75.9%) and yearling coho salmon and adult Chinook salmon (74.3%). Cluster groups B and D had the highest overlap (mean 46.9 and 52.8%, respectively), with group C (surf smelt and market squid) having a mean overlap of 31.1%. Within groups B and D, euphausiids accounted for 95 and 55%, respectively of total overlap among nekton. For August 2000 (Table 2.8), highest overlap values were between yearling coho and adult Chinook salmon (85.8%), jack mackerel and juvenile steelhead trout (77.7%), and adult Chinook and adult coho salmon (71.8%). Mean overlap within trophic groups were 66.4, 39.9, and 45.2 for groups A, B and C, respectively. Prey accounting for most overlap in diet of group A were adult fish (77% of total overlap within group), and larval and juvenile fish (22%). Group B overlap was primarily due to larval and juvenile fish (~80% of total overlap), followed by adult euphausiids (~15%), and group C overlap was dominated by euphausiids (97%). During June 2002 (Table 2.9) no species pairs had similarities in diet >60%, with yearling Chinook and yearling coho salmon, and Pacific sardine and juvenile

Table 2.6. June and August 2002 summary of results from Indicator Species Analysis (ISA) of cluster groups based on agglomerative hierarchical cluster analysis of nekton diets. Life history stages of nekton and prey are in parentheses and represent: egg (e), megalopa larvae (m), larva (l), juvenile (j), furcilia (f), yearling (y) and adult (a); nekton and prey with no indication of life history stage are adult.

Cruise Period Nekton Species	Cluster Group	Indicator Prey Species	Indicator Value	p-value
June 2002				
Pacific Hake	E	*Cancer magister* (m)	51.0	0.241
Chinook (a)	E	*Euphausia pacifica*	76.3	0.223
Spiny Dogfish	E	Euphausiidae	35.7	0.674
Jack Mackerel	E	Gelatinous material	71.7	0.222
		Osteichthyes (a)	50.0	0.196
Pacific saury	D	Brachyura (l, J)	33.7	0.757
Chum salmon (j)	D	Osteichthyes (e)	73.9	0.131
Chinook salmon (y)	D	Osteichthyes (j)	57.9	0.044
Coho salmon (y)	D			
Market squid	C	-		
Pacific sand lance (j)	B	*Cancer* spp. (l)	45.5	0.315
Pacific herring	B	Decapoda (l, j)	35.5	0.505
Steelhead trout (j)	B	Hyperiidea	91.3	0.066
		Thysanoessa spinifera	83.4	0.003
Widow rockfish (j)	A	Appendicularia	28.5	0.639
Pacific sardine	A	Copepoda	89.2	0.036
		Euphausiidae (e)	94.8	0.028
		Euphausiidae (f)	64.8	0.098
August 2002				
Chinook salmon (y)	C	Cancer magister (m)	71.4	0.262
Northern anchovy	C	*Euphausia pacifica*	85.7	0.086
Jack mackerel	C	Euphausiidae	96.5	0.033
Chinook salmon (a)	C	Hyperiidea	58.7	0.578
Pacific herring	C	Osteichthyes (a)	14.3	1.000
Sablefish (j)	C	Osteichthyes (j)	97.1	0.063
Coho salmon (y)	C	*Thysanoessa spinifera*	99.8	0.033
Market squid	B	Cephalopoda	45.1	0.243
Pacific saury	B	Copepoda	47.3	0.218
		Gelatinous material	100.0	0.033
Blue shark	A	-		

widow rockfish having the highest level of overlap (58% for both). Highest mean overlap occurred within cluster group E (58%), followed by C (28%), B (17%) and A (15%). Within group similarities in diet were primarily attributed to copepods (93% of total similarity) for group A, adult euphausiids (58%) for group B, juvenile Osteichthyes (90%) for group C, and adult fish and larval and juvenile fish (41 and 20%, respectively) for group D. For August 2002 (Table 2.10) highest overlap occurred within group A with adult Chinook and Pacific herring, adult Chinook and juvenile sablefish, and Pacific herring and juvenile sablefish, having percent overlaps of 83.7, 78.7 and 74.1%, respectively. Mean overlap within group A was 50% and for group B 10%. Euphausiids accounted for ~90% of the total similarity in diets within group A, whereas group B similarities were primarily gelatinous material (90%) and euphausiids (10%).

Trophic Distribution and Environment

Cluster analysis of predator-station x prey matrixes and application to NMS with an environmental matrix allowed for visual inspection of the spatial distribution of prey consumed relative to environmental parameters. For June 2000, cluster analysis groupings were cut at 37% level of information remaining, resulting in four significant groups (MRPP A=0.35, $p<<0.0001$). A 3-dimensional NMS ordination (stress=15.8, final instability = 0.0002) was able to explain 65% of the variation, with axis 1 and 3 explaining 20 and 24%, respectively. A gradient along axis 1 with respect to chl-*a* (Fig. 2.5) was observed. Only two of the four groups were well-separated along this axis. The group most positively correlated with chl-*a* consisted of adult Chinook salmon, and to a lesser extent Pacific herring, yearling coho salmon and market squid (group 1, Fig. 2.5). Only one indicator prey species, *T. spinifera*, was significant (ISA, p=0.001). The group most separate from chl-*a* consisted of market squid, surf smelt, Pacific herring, and to a lesser extent, whitebait smelt and juvenile rockfish species (group 4, Fig. 2.5). Indicator species analysis of prey within this group revealed significant prey species of larval juvenile crustaceans (decapods, brachyuran, *Cancer* spp.), copepods, euphausiid eggs, and hyperiid amphipods. Two mid-groups consisting primarily of yearling and adult

Table 2.7. June 2000 percent similarity index (PSI, Eqn. 1) of nekton diets from the northern California Current (NCC). Cluster groups were derived from agglomerative hierarchical cluster analysis (AHCA) of percent wet weight of diet. Blocked PSI values denote within cluster group comparisons. PSI values >60% are in bold. Life history stages of nekton are in parentheses and represent juvenile (j), yearling (y) and adult (a); nekton with no indication of life history stage are adult.

Cluster Group		Chinook (y)	Coho (y)	Steelhead trout (a)	Chinook (a)	Market squid	Surf smelt	Whitebait smelt	Pacific herring	Sablefish (j)	Lingcod (j)
D	**Chinook (y)**	X									
	Coho (y)	29.7	X								
	Steelhead Trout (j)	30.1	**70.1**	X							
	Chinook (a)	36.5	74.3	**75.9**	X						
C	**Market Squid**	28.7	45.1	53.5	56.0	X					
	Surf Smelt	5.1	8.3	6.5	6.2	31.1	X				
B	**Whitebait Smelt**	7.6	43.3	**69.5**	50.7	33.3	5.9	X			
	Pacific Herring	7.6	38.3	61.3	44.1	42.0	21.9	**79.2**	X		
	Sablefish (j)	1.0	9.6	6.1	10.2	0.0	6.2	33.6	28.0	X	
A	**Lingcod (j)**	1.0	4.4	4.1	4.0	4.7	9.8	5.2	6.3	0.0	X

Table 2.8. August 2000 percent similarity index (PSI, Eqn. 1) of nekton diets from the northern California Current (NCC). Cluster groups were derived from agglomerative hierarchical cluster analysis (AHCA) of percent wet weight of diet. Blocked PSI values denote within cluster group comparisons. PSI values >60% are in bold. Life history stages of nekton are in parentheses and represent juvenile (j), yearling (y) and adult (a); nekton with no indication of life history stage are adult.

Cluster Group		Blue Shark	Coho (a)	Surf Smelt	Coho (y)	Chinook (y)	Chinook (a)	Pacific mackerel	Pacific saury	Pacific sardine	Jack mackerel	Steelhead trout (j)
C	**Blue shark**	X										
	Coho (a)	**66.4**	X									
B	**Surf smelt**	1.8	1.9	X								
	Coho (y)	24.4	18.1	5.9	X							
	Chinook (y)	35.6	28.5	4.3	**68.9**	X						
	Chinook (a)	26.0	16.8	2.5	**85.8**	**71.8**	X					
A	**Pacific mackerel**	23.5	5.0	2.0	6.9	8.8	10.2	X				
	Pacific saury	25.6	2.2	1.1	5.1	6.0	8.0	59.4	X			
	Pacific sardine	5.1	0.3	2.2	1.6	0.7	1.0	0.2	33.4	X		
	Jack mackerel	25.6	3.2	1.3	12.0	13.1	15.2	29.7	**62.4**	56.6	X	
	Steelhead trout (j)	23.0	5.5	9.2	16.0	15.5	14.9	16.9	48.6	**66.8**	**77.7**	X

Table 2.9. June 2002 percent similarity index (PSI, Eqn. 1) of nekton diets from the northern California Current (NCC). Cluster groups were derived from agglomerative hierarchical cluster analysis (AHCA) of percent wet weight of diet. Blocked PSI values denote within cluster group comparisons. PSI values >60% are in bold. Life history stages of nekton are in parentheses and represent juvenile (j), yearling (y) and adult (a); nekton with no indication of life history stage are adult.

Cluster Group		Jack mackerel	Spiny dogfish	Chinook (a)	Pacific hake	Coho (y)	Chinook (y)	Chum (j)	Pacific saury	Market squid	Steelhead trout (j)	Pacific herring	Pacific sand lance	Pacific sardine	Widow rockfish (j)
D	**Jack mackerel**	**X**													
	Spiny dogfish	5.4	X												
	Chinook (a)	32.8	2.7	X											
	Pacific hake	5.6	3.2	40.6	X										
C	**Coho (y)**	24.2	2.5	25.5	2.9	X									
	Chinook (y)	21.6	1.2	22.2	1.7	58.7	X								
	Chum (j)	19.6	1.8	20.7	2.3	20.7	24.4	X							
	Pacific saury	24.3	0.0	24.5	0.2	30.5	27.8	20.0	X						
B	**Market squid**	4.5	0.3	1.4	0.9	0.4	7.5	4.9	0.0	X					
	Steelhead trout (j)	30.3	3.3	20.8	11.1	36.8	35.1	23.1	26.2	0.3	X				
	Pacific herring	17.6	3.4	10.2	11.7	10.5	15.5	14.6	5.8	11.4	28.6	X			
	Pacific sand lance	4.4	2.4	4.1	7.3	5.1	4.7	7.3	1.0	2.6	26.1	30.4	X		
A	**Pacific sardine**	2.5	0.8	1.4	1.0	0.8	0.9	5.8	0.3	0.3	2.7	12.2	12.3	X	
	Widow rockfish (j)	15.0	0.7	13.1	2.2	13.2	12.7	14.3	12.4	0.2	14.8	28.6	12.0	58.3	X

Table 2.10. August 2002 percent similarity index (PSI, Eqn 1) of nekton diets from the northern California Current (NCC). Cluster groups were derived from agglomerative hierarchical cluster analysis (AHCA) of percent wet weight of diet. Blocked PSI values denote within cluster group comparisons. PSI values >60% are in bold. Life history stages of nekton are in parentheses and represent juvenile (j), yearling (y) and adult (a); nekton with no indication of life history stage are adult.

Cluster	Group	Blue shark	Market squid	Pacific saury	Chinook (y)	Northern anchovy	Jack mackerel	Chinook (a)	Pacific herring	Sablefish (j)	Coho (y)
C	**Blue shark**	X									
B	**Market squid**	0.3	X								
	Pacific saury	0.0	10.1	X							
A	**Chinook (y)**	0.0	1.0	1.7	X						
	Northern anchovy	0.0	1.0	1.2	33.4	X					
	Jack mackerel	0.1	1.2	1.6	33.9	34.1	X				
	Chinook (a)	0.0	1.0	1.5	54.7	58.2	45.3	X			
	Pacific herring	0.0	1.0	3.9	43.0	55.5	42.4	**83.7**	X		
	Sablefish	0.0	1.0	1.9	35.3	**60.5**	35.9	**78.7**	**74.1**	X	
	Coho (y)	27.1	1.0	2.0	45.5	46.1	31.7	57.9	51.3	50.8	X

Chinook salmon and yearling coho salmon (group 2 and 3, respectively) were indistinguishable along axis 1, however they both tended to cluster toward higher chl-*a* levels (Fig. 2.5). Indicator prey species for these groups were adult euphausiids, *Euphausia pacifica*, and larval-juvenile Osteichthyes.

Cluster analysis of August 2000 resulted in four significant cluster groups (MRPP A=0.28, p<<0.0001) with 35% information remaining. A 3-dimensional NMS result was able to explain 54% of the variation in the data, most occurring along axis 2 (17%) and 3 (22%). Stress was 16.9 (final instability << 0.0001) indicating moderate structure to the data. Distance offshore was the only significant environmental parameter related to axis 2 (Fig. 2.6). Of the four cluster groups one was highly correlated to distance offshore (group 1, Fig. 2.6), consisting of adult coho and blue shark. Adult Osteichthyes was the only significant indicator prey species for this group. Two mid-groups (groups 2 and 3, Fig. 2.6) along axis 2 consisted primarily of jack mackerel, juvenile steelhead trout and yearling coho salmon, and another group of yearling and adult Chinook salmon and also yearling coho salmon. Primary indicator prey for these groups consisted largely of adult euphausiids, *E. pacifica* and *T. spinifera*, and larval-juvenile osteichthyes, respectively. A nearshore group (group 4, Fig. 2.6) consisting primarily of Pacific sardine, yearling Chinook and coho salmon, and juvenile steelhead trout had the highest richness of prey species diversity (n=20 out of 25 total) and the highest number of significant indicator prey species (n=11). The most significant prey were copepods (p=0.003), hyperiid amphipods (p=0.007) and decapod larvae (p=0.01).

June 2002 cluster analysis resulted in three significant groups (MRPP A= 0.51, p<<0.0001) at the cutoff level of 48% information remaining. A 3-dimensional NMS ordination (stress=15.8, final instability = 0.001) was able to explain 83% of the variation, most occurring along axis 1 (43%) and 3 (24%). Along axis 1, water depth was the only significant environmental parameter (Fig. 2.7). Two of the three cluster groups were more negatively correlated with depth (groups 2 and 3, Fig 2.7). Both groups primarily consisted of yearling coho and Chinook salmon, and adult Chinook salmon.

The group most positively correlated with depth had a broad range of species (group 1, Fig. 2.7), with the most frequent being Pacific sardine, Pacific herring, pelagic juvenile rockfish and juvenile Pacific sand lance. Indicator species analysis revealed that the more shallow-depth groups had significant indicator prey species of larval-juvenile Osteichthyes and *Cancer magister* megalopae. The offshore group contained the most indicator prey species, with copepods, larval-juvenile decapods, brachyuran larvae, euphausiids and T. *spinifera*, Osteichthyes eggs and hyperiid amphipods all being significant.

Cluster analysis of August 2002 resulted in four significant groups (MRPP A=0.40, $p<<0.0001$) at a cutoff of 28% information remaining. A 3-dimensional NMS ordination was able to explain 89% of the variation (stress 13.9, final instability = 0.005, 500 iterations), with most occurring along axis 1 and 2 (24 and 47%, respectively). A joint plot revealed parameters distance offshore and salinity to be significant along axis 1 (Fig. 2.8). Group distribution within this plot, however, was better described along axis 2. Along the distance offshore and salinity gradient of axis 1, two groups were distinctly different, with one distributed farther offshore and the other strongly associated with higher salinities (group 1 and 4, Fig. 2.8, respectively). The most offshore group consisted of yearling Chinook, market squid, and to a lesser extent Pacific saury, subyearling Chinook and yearling coho salmon. Only one significant indicator species, larval-juvenile Osteichthyes, was listed for this group. The high-salinity specific group contained mostly yearling and adult Chinook salmon and to a lesser extent Pacific herring. Only one significant indicator prey species was observed, *T. spinifera*. The remaining two groups separated along axis 2 (group 2 and 3, Fig. 2.8), showed little trend with respect to the environmental variables. Predators within these groups were primarily yearling coho and Chinook, adult Chinook, Pacific herring and juvenile steelhead. Significant indicator species were euphausiids, *E. pacifica*, *Cancer magister* megalopae, copepods and hyperiid amphipods.

Seasonal and Interannual Variation

Comparison of diets from June and August 2000 and 2002 showed considerable seasonal variation in percent weight contribution to diet. During June 2000, euphausiids comprised >70% (wet weight) of the diets of yearling coho and adult Chinook; this pattern was reversed during August with larval-juvenile fish contributing >75% of the diet (Fig. 2.9). In contrast larval-juvenile fish contributed more to percent wet weight of yearling Chinook during June (>90%) and slightly less during August (~70%). For juvenile steelhead trout larval and juvenile fish contributed substantially to percent wet weight of diet during June (~20%) relative to August (~2%); euphausiids were consistently high for both periods, contributing ~75% and 85% to June and August diets, respectively. Surf smelt showed only a small difference between periods with more hyperiids consumed in August. The stomach contents of surf smelt during August were more well-digested compared to June (mean digestion of 2.0, and 2.5, respectively) resulting in a higher contribution of crustacean tissue to diet (Fig. 2.9, Appendix A), as opposed to more refined prey categories. Other than this difference, surf smelt consumed more cnidarians (polyp larvae) in June and more *Cancer* sp. larvae in August. During 2002 yearling Chinook and coho salmon had very similar trends in diets between June and August, with more fish (>80%) consumed in June compared to August (>40% for both)(Fig. 2.10). During August, euphausiids comprised ~ 50% of yearling coho and Chinook salmon diets. Adult Chinook salmon, jack mackerel and Pacific herring generally contained more diverse diets in June with lower weight contribution of adult euphausiids relative to August. During August, >80% of adult Chinook and Pacific herring diets consisted of euphausiids and jack mackerel diets contained ~45% euphausiids, with remaining prey only distinguished as crustacean material.

Interannual comparison of yearling and adult Chinook, and yearling coho salmon showed larval-juvenile fishes, adult fishes and adult euphausiids consistently contributed >90% of the diet for both years, with the remaining dominant prey items, brachyuran and *Cancer magister* larvae, varying by year (Fig. 2.11). For adult and yearling Chinook, adult and larval-juvenile fish were collectively the dominant prey by weight during 2000 (~53%

and 80%, respectively). During 2002, adult Chinook salmon diet contained a higher percent wet weight of adult fishes (18%), euphausiids (~40%) and C. *magister* larvae (7%), whereas yearling Chinook salmon consumed higher percentages of larval-juvenile fishes (66%), euphausiids (~28%) and brachyuran larvae (4%) relative to 2000. Yearling coho salmon had higher percent wet weights of adult and larval-juvenile fishes (10% and 34%, respectively) during 2002 and euphausiids contributed higher percent wet weight (~44%) during 2000.

Interdecadal Comparison

Comparison of juvenile Chinook diets from our study (2000 and 2002) to Brodeur and Pearcy's (1992) assessment from the 1980s showed Osteichthyes (larval and juvenile) were proportionally the most dominant prey item (>60%) for all years (Fig. 2.12), with the remaining proportion of diet coming from other relatively minor groups. During the 1980s, these minor prey were more diverse, including cephalopods, decapods, euphausiids, copepods and pteropods; during 2000 and 2002, minor prey items were primarily euphausiids, amphipods, and decapods. A 3-dimensional NMS ordination of predator/year by prey species with respect to percent wet weight contribution to diet was able to explain 76% of the variation (stress = 15.9, final instability = 0.0007), with most occurring along axis 2 and 3 (27 and 31%, respectively). This difference is expressed in the NMS joint plot, with distinct separation of 2000 and 2002 from the 1980s, particularly from 1981 and 1984 (Fig. 2.13). This separation was largely due to the higher contribution by decapod larvae and chaetognaths to 1980s diets and amphipods during 2000 and 2002. Adult Chinook salmon diets varied more interannually, primarily due to differences in the relative contribution of larval-juvenile fish and euphausiids. With the exception of 1981, the 1980s had more diverse diets compared to 2000 and 2002. During 1982-1984, after Osteichthyes and euphausiids, the primary prey were decapods and cephalopods, whereas only amphipods were proportionally noticeable during 2000 (10%). An NMS joint plot (Fig. 2.13) shows the primary difference between the 1980s and 2000s is due to the increased presence of decapods and cnidarians during the 1980s.

A similar trend to juvenile Chinook was observed with juvenile coho salmon, with fish consistently contributing to the highest proportion of diet (>40%). Overall juvenile coho salmon exhibited a higher dietary diversity during the 1980s with decapod larvae, euphausiids, chaetognaths, amphipods and pteropods contributing mostly to the remaining proportion of the diets, depending on year. During 2000 and 2002, euphausiids, decapods and amphipods were the only prey contributing to the diet after

Osteichthyes. An NMS joint plot shows 2000 juvenile coho salmon separated from the 1980s fish, primarily due to the importance of amphipods in the diet in 2000 fish and decapod larvae in 1981, 1983 and 1984 (Fig. 2.13). No data were available for jack mackerel from 1981, with comparisons between the 1980's and 2000's being between 1982-1984 and 2000 and 2002 fish. With the exception of 1982, when Osteichthyes were the dominant prey (>80%), euphausiids were consistently the dominant prey taxa (>80%). Small differences were observed among minor prey items between the 1980s and 2000s. NMS joint plot showed 1983, 2000, and 2002 diets were most similar, with euphausiids being the most significant prey taxa, compared to 1982 and 1984, which were more correlated with Osteichthyes and chaetognaths, respectively (Fig. 2.13).

DISCUSSION

This study provides baseline information on diets of 25 dominant marine nekton of the NCC system during a cool productive regime phase (Peterson and Schwing 2003), and examines the trophic relationships among these species and their environment. Statistical comparisons of diets, however, were limited to 22 species due to the limited number and frequency of occurrence of some species for analysis.

Trophic Relationships

Trophic categories assigned by cluster analysis provided a measure of the relative trophic position of nekton within a cruise and a measure of the degree of overlap between individual species. Lowest trophic levels included Pacific sardine, juvenile rockfish and

juvenile lingcod that typically consumed copepods, euphausiid eggs and furcilia. For juvenile rockfish this generally agrees with a previous study on juvenile rockfish diets from the southern California Current (Reilly et al. 1992). However, some species of juvenile rockfish (widow and darkblotched) and juvenile lingcod also consumed larger prey such as adult euphausiids, and other larval-juvenile fishes. Although Pacific sardine were assigned to a lower trophic group (June 2002 period), we also observed feeding on adult euphausiids (June and August 2000), indicating this species is more euryphagous than other planktivores within this group. Pacific sardine have been observed to feed on phytoplankton, copepods and euphausiids within the southern part of the California Current (Southern California and Baja California, Hand and Berner 1959), the NCC (Hart and Wailes 1931) and Gulf of Alaska (Wing et al. 2000) ecosystems. Van Der Lingen (2002) observed *S. sagax* to feed more exclusively on smaller crustacean zooplankton (e.g. copepods), along with phytoplankton, in the southern Benguela Current ecosystem. The lowest trophic level group observed in this study had species that were apparently limited by gape size to smaller prey (as in juvenile fish), with Pacific sardine expressing a broader size-based diet (Van Der Lingen 2002).

For all cruises the middle trophic groups comprised the highest number of predator species examined, generally consisting of Pacific herring, smelts (surf and whitebait), Pacific sand lance, market squid, and mackerel (jack and Pacific), with ISA of prey indicating these mid-trophic groups generally consumed adult euphausiids, decapod and brachyuran larvae. With the exception of June 2002, euphausiids were the dominant prey of this group, with minor prey items accounting for ~30% (wet weight) of the diet of most species. Brodeur et al. (1987) observed euphausiids to be an important prey of Pacific herring, jack and Pacific mackerel. To the north of our study area (off the Columbia River), an extensive analysis of jack mackerel stomachs over an 7 yr period showed euphausiids, and to a lesser degree small fishes, to be the dominant prey taxa by occurrence (R. Emmett, NMFS pers. comm.). *Trachurus trachurus* (horse mackerel) from the southern Benguela ecosystem also appears to feed predominantly on euphausiids and ichthyoplankton (Pillar and Barange 1998). Market squid from our study

area showed a diverse diet of crustacean prey (decapod larvae, euphausiids, fish and other cephalopods), which is in general agreement with other diet studies on *Loligo* (Macy 1982, Brodeur et al. 1987, Collins et al. 1994).

Juvenile salmonids generally clustered into a mid-upper trophic group, feeding primarily on larval-juvenile fish and euphausiids. The diets of juvenile salmonids have been well studied within the NCC system (e.g. Peterson et al. 1982, Brodeur and Pearcy 1990, Brodeur et al. 1992, Schabetsberger et al. 2003, Brodeur et al. in prep.). Major prey of juvenile Chinook and coho salmon tend to be ichthyoplankton, with coho tending to have a higher proportion (by wet weight) of decapod larvae and euphausiids relative to Chinook salmon. In both species the combined contribution of fish and euphausiids is usually over 70-80% wet weight of diet (Brodeur et al. in prep.), which is consistent with the results observed here. Juvenile salmonids therefore represent a mid-upper trophic group consuming ichthyoplankton and larger crustacean prey (e.g. euphausiids and decapod larvae).

When present, upper trophic groups consisted of adult blue shark (August 2000) and Pacific hake (during June 2002), with adult Chinook and coho salmon at times showing both upper and mid-trophic level feeding behavior. Blue shark and hake appeared to be largely piscivorous within this study; however some portion of their diet consisted of adult euphausiids. Harvey (1989) observed blue sharks to consume euphausiids (primarily *T. spinifera*) and adult fish. Brodeur et al (1987) observed blue shark to consume almost entirely adult fish with some cephalopod beaks present in the diet; we also observed cephalopod beaks (Appendix A) but no obvious presence of soft tissue. Diets of adult hake within the NCC have shown that they feed predominantly on euphausiids and other fish (Tanasichuk 2002, R. Emmett pers. comm.). In comparing hake diets from the California, Benguela and Peruvian upwelling ecosystems, Ware (1992), observed hake to generally feed on fish and euphausiids, but that euphausiids contributed more to the diet of hake from the California Current ecosystem compared to the other systems. Adult Chinook and coho salmon diets also consisted of adult and

larval-juvenile fish and euphausiids with most of their diet (wet weight) consisting of larval-juvenile fish and euphausiids. Brodeur et al. (1987) observed fish contributing the highest proportion to adult coho and Chinook diets, with euphausiids, squid and other invertebrates contributing to the remaining portion of diet. Hunt et al. (1999) found adult Chinook salmon consumed predominantly adult fishes, *Clupea pallasii* and *Engraulis mordax*, and the adult *T. spinifera* off northern California. Welch and Parsons (1993) and Kaeriyama et al. (2004) observed high nitrogen stable isotope values in adult coho and particularly in Chinook salmon, which concur with observations from diet studies that they occupy a higher trophic level.

The high number of nekton species in the mid-trophic group is consistent with the trophic structure of other systems including the Western Atlantic (Link 2002). This group generally consumed more euphausiids than other groups and the frequent assignment of various eupahusiid life stages as indicator species to multiple trophic groups indicates the importance of this prey at this time. Juvenile rockfish and adult sardine, saury, surf smelt all had some component of their diet consisting of euphausiid eggs and furcilia. Middle and upper trophic groups had diets consisting of adult euphausiids, *T. spinifera* and *E. pacifica*, which accounted for most of the interspecific diet overlap (Table 2.7-2.10). The relative dominance of euphausiids in the diets of so many species observed here may be explained by their aggregation patterns. Euphausiids off Oregon and northern California have been shown to be concentrated around the shelf break and submarine banks, with low densities elsewhere (Ressler et al. 2005, Swartzman et al. 2005). Yet many of the nekton consuming euphausiids within this study were collected over a broad spatial (cross-shelf and latitudinal) scale (see Distribution section below), indicating these major aggregations of euphausiids are not the only major source for predators. From multibeam sonar tracking of zooplankton and fish in Saanich Inlet (Vancouver Island, Canada) Jaffe et al. (1999) observed no discernable horizontal overlap in aggregations of euphausiids and Pacific herring, although euphausiids are known as important prey of Pacific herring from this region (Robinson 2000). The contribution of euphausiids to many nekton species may be due to recent increases in euphausiid abundance since 1999 euphausiids

within the NCC system. Feinberg and Peterson (2003) observed an extension in the season of euphausiid spawning and multiple peaks in egg density starting in 1999, presumably when there was a shift in the production regime. Swartzman and Hickey (2003) observed an increase in euphausiid abundance south of Cape Blanco and greater aggregation along the shelf during 2001 relative to years 1995 and 1998. Brodeur et al. (In prep.) examined the diets of juvenile coho salmon from 1980-1985 and 1998-2003 and, although interannually variable, there appeared to be a slight (non-significant) increase in the contribution of euphausiids to the diets of juvenile coho salmon between these two production regimes. Making a case for increased euphausiid availability to higher trophic levels in the latter period is problematic because of the extreme patchy nature of adult stages in relation to currents and bathymetry (Ressler et al. 2005), differences in productivity and latitudinal abundance (Ware and Thomson 2005), and predator-prey relationships (Mackas et al. 1997) across production regimes.

Trophic Patterns and Environment

For all cruises results from NMS of predator/station by prey matrix showed at least one cross-shelf related environmental parameter associated with structure in the data. Parameters most associated with the distribution in diets of nekton were chl-*a* (June 2000), distance offshore (August 2000 and 2002), depth (June 2002) and salinity (August 2002), with higher chl-*a* values and salinity associated with more nearshore stations and increasing depth and distance offshore associated with offshore stations. The irregularity of parameters between cruises indicates the spatial dynamics of this system where upwelling can be associated with increased salinity nearshore from newly upwelled water (Huyer 1983, Barth et al. 2005), and over some time-lag an associated phytoplankton bloom (Small and Menzies 1981). Increasing depth with distance offshore is associated with the geomorphology of the shelf where depth markedly increases at the shelf break with increased distance from shore.

The general cross-shelf patterns in consumed prey from each cruise reflects the prevailing cross-shelf distributions observed in zooplankton (Morgan et al. 2002, Peterson and

Keister 2002, Reese et al. 2005), pelagic larval and juvenile fishes (Richardson and Pearcy 1977, Brodeur et al. 2003, Emmett et al. 2005) and adult nekton (Brodeur and Pearcy 1986, Brodeur et al. 2003) within this system. No consistent trend was observed in the cross-shelf distribution of feeding groups between different cruises, indicating the spatially and temporally dynamic nature of this system. Some species that are known to be more offshore species (e.g. blue shark, Pacific mackerel and Pacific saury) showed a strong affinity to offshore groups in our study (Brodeur et al. 2004). Other more abundant species of nekton were less defined to any particular group. Brodeur and Pearcy (1992) spatially divided the NCC ecosystem food web into inshore, mid-shelf and offshore organisms (phytoplankton to adult fish), with species and trophic levels crossing over spatial assignments. In this conceptual model the spatial distribution varied by year indicating the dynamic nature of organism distribution and trophic links within a moving (fluid) environment. Much of this variation is likely associated with upwelling and the interaction between nearshore and offshore (California Current) waters, and the temporal response of organisms to changes in the system. Unlike nekton that can swim against ocean currents, zooplankton are more prone to advection and therefore have been well associated with cross-shelf differences in community structure within the NCC ecosystem (Reese et al. 2005, Ressler et al. 2005). Certain species tend to associate with specific water masses (Brodeur et al. 2004), fronts (De Robertis et al. 2005) or in apparent proximity to prey (Mackas et al. 1997, Tynan et al. 2005). Sampling and collection of fish for diet analysis was opportunistic within our study area and therefore limited the distribution of data relative to extremes in environmental conditions (e.g. temperature, salinity and chl-*a*). A more meaningful method for revealing predator-prey interactions relative to environmental parameters using NMS would have been to obtain larger sample sizes across a broader temporal and spatial scale (discussed below) to capture the extremes in abiotic and biotic measures.

Temporal - Seasonal/interannual Variation

Nekton displayed a high degree of seasonal and interannual variation in diets. For salmonids much of this variation was attributed to shifts in the dominance of euphausiid

and fish prey, whereas non-salmonids displayed higher diversities in diets that varied by multiple prey. For salmonids seasonal differences in prey during 2000 showed adult Chinook and juvenile coho salmon to consume primarily euphausiids in June (>60% damp weight contribution to diet) and fishes in August (>70%) In contrast, yearling Chinook consumed more fish (>90%) in June than August (~65%). Surf smelt showed a highly diverse diet (Fig. 2.9) during both cruises and juvenile steelhead consistently had euphausiids as the dominant (>70% wet weight) prey. The high contribution of euphausiids to juvenile coho was also observed by Brodeur et al. (in revision), during the same general period to the north (central Oregon to northern Washington) of our study area. During 2002 we observed greater consistency in diets of all nekton across season, with more larval-juvenile fishes and decapod larvae (Brachyura, and *Cancer* sp. combined) consumed during June and euphausiids in August. Brodeur et al. (in revision) observed less variation in juvenile coho salmon, with fish consistently contributing to >78% by weight during June and September; for our study euphausiids contributed to 43% by weight of juvenile coho salmon diets during August.

Interannual comparisons of diets between 2000 and 2002 of yearling and adult Chinook, and yearling coho salmon showed that larval-juvenile fishes and euphausiids consistently contributed to most of the diet, with variation occurring between these prey groups. Fish were more important in the diets of yearling and adult Chinook salmon in 2000, whereas yearling coho salmon consumed more euphausiids in 2000. Decapod larvae were relatively more important in the diets of all nekton compared during 2002. Brodeur et al (in revision) observed slightly more elevated percentages of decapods in juvenile coho salmon diets during 2002, consistent with our observations. Brodeur and Pearcy (1992) observed that highest dietary overlap among nekton occurred during 1982, a strong upwelling year, and that euphausiids accounted for much of this overlap. Our study occurred during a period of above average upwelling during both years (Fig. 2.14), which may explain the overall importance of euphausiids in the diets of salmonids and other species resulting in high dietary overlap. Indeed, due to an intrusion of cool, high nutrient Subarctic waters in August 2002, chlorophyll concentrations were extremely

high in surface waters, which subsequently led to settling of unconsumed organic matter and hypoxia in near-bottom waters (Grantham et al. 2004). There were not any readily observed repercussions of this event in the diets of these pelagic predators.

Interannual variability in diets can be attributed to a number of factors, including overall variability of certain prey over a broad temporal and spatial scales, aggregation of prey due to physical processes (Ressler et al. 2005), ability of predators to locate prey at different levels of water clarity (De Robertis et al. 2003), diurnal feeding patterns and prey avoidance **(**De Robertis et al. 2000), and/or an artifact of sampling. Dorman et al. (2005) observed significant levels of interannual variation in the abundance of *E. pacifica* off northern California between June 2000 (higher) and May-June 2001. This was attributed to decreased upwelling during 2000 which allowed for favorable ocean conditions for euphausiid recruitment. In contrast Ainley et al. (1996) observed a positive link between upwelling and *T. spinifera*. Therefore interannual variability in euphausiid abundance is difficult to ascertain from predator diets because of the problems associated with predator-prey aggregation and a changing environment. Further study is needed however to better understand this important aspect of large marine food webs.

Interdecadal Comparison

Our comparison of juvenile and adult Chinook, juvenile coho and jack mackerel analyzed from GLOBEC 2000 and 2002 cruises to collections and analysis from Brodeur and Pearcy (1992) showed little interdecadal difference in major prey items. Euphausiids and larval-juvenile fish were almost always the two most dominant taxa, with minor species varying from year to year. Interannual differences rather than interdecadal accounted for much of this variation. Brodeur et al. (in revision) also compared diets of juvenile coho salmon from the 1980-1985 to those analyzed from 1998-2003 within the same general area. They observed much stronger interannual than interdecadal variation in the diets, with larval and juvenile fishes and euphausiids contributing the most to the diet and varying from year to year. Comparison of dietary overlap results from our study to Brodeur and Pearcy (1992) during the 1980s showed few differences, with interannual

variation exceeding any interdecadal trend. The apparent lack of difference between the two periods is contrary to assumed bottom-up forcing from a regime shift perspective where abiotic forcing causes shifts in primary production eventually leading to increased food for salmonids (e.g. Gargett 1997, Ware and Thomson 2005) and other nekton. Possibly the mechanisms at play are not reflected in diets at the time of our studies (i.e. late spring and summer months) and that the methods of dietary analysis alone, without including dimensions of predator and prey biomass, cannot reveal mechanisms of bottom-up or top-down patterns in the system. Moreover, if we examined dietary differences on a finer prey resolution, we might expect to see some differences not evident at the coarser scale that we used. For example, among the prey juvenile fish species we observed, we noted that sardines are a common feature of the diets in the recent sampling and were barely present in our ecosystem in the 1980s (Emmett et al. 2005).

Comparison to Other Ecosystems

Our results provide a detailed, yet broad view of trophic connectivity of nekton within the NCC ecosystem. A comparison of the diets of major nekton indicative of upwelling regions (e.g. horse/jack mackerel, sardine, anchovy, and hake) may provide the best direct comparison of ecosystem food webs to our study of the NCC. Results from our study as well as previous studies within the NCC indicate euphausiids are an important food source for the most abundant nekton (Brodeur et al. 1987, Ware 1992, Robinson 2000, Tanasichuk 2002). Hake from all major upwelling ecosystems consume fish and euphausiids, with euphausiids contributing considerably more of the diet from the California Current (Ware 1992). Jack mackerel from the NCC consume primarily euphausiids, which has been observed in other *Trachurus* spp. from the Benguela Current (Pillar and Barange 1998) and other non-upwelling regions (Santic et al. 2004 – Adriatic Sea). Diets of *Sardinops sagax* from the Benguela ecosystem primarily consisted of smaller crustacean zooplankton and phytoplankton (Van Der Lingen 2002) than observed in the California Current system. Of the major upwelling systems, the California Current is considered to be the least productive and least efficient in terms of trophic transfer

from primary production to fishes (Ware 1992). The apparent differences between ecosystem trophic patterns and links may be important in better understanding community stability/complexity and resistance to perturbations.

Interannual and interdecadal comparisons of species distribution and community structure of pelagic nekton have demonstrated that the northern California Current system can vary of different time scales but also shows some resilience due to a high degree of species complimentarity (Reese 2005). As fishery management continues to shift away from single species towards multispecies or ecosystem-based fishery management (Browman and Stergiou 2004, Pikitch et al. 2004) including the NCC (Bottom et al. 1993, Field et al. 2001), detailed information on the trophic interactions within this pelagic ecosystem as presented here will become indispensable. Further analysis of the major nekton and their prey is warranted to elucidate differences in trophic functioning between major upwelling regions and within regions under the influence of climatic variability.

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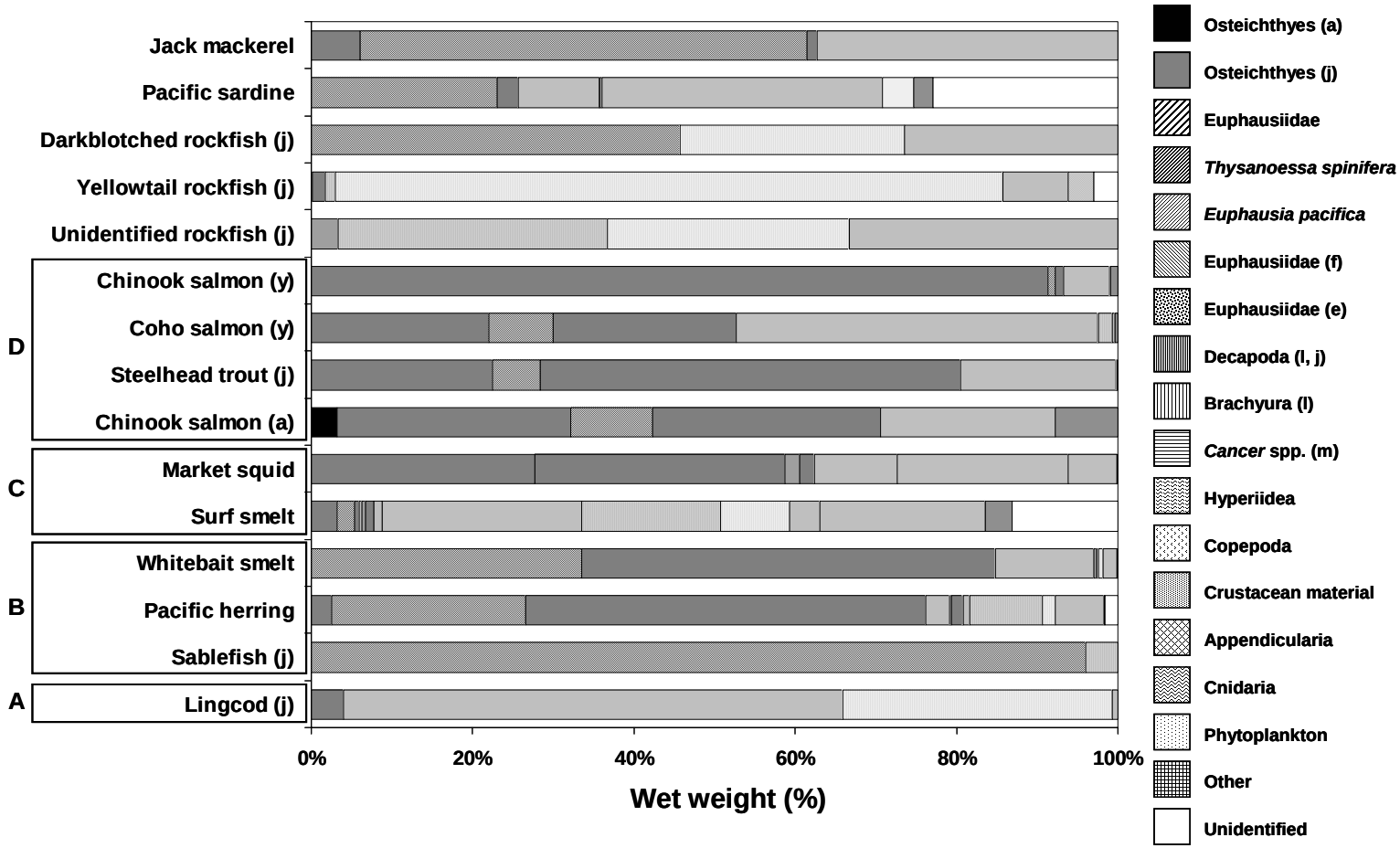

Figure 2.1. June 2000 nekton diets. Groups based on cluster analysis of diets (% wet weight) are blocked and labeled by low (A) to higher (D) trophic groups. Species not blocked lacked sufficient numbers and frequency of occurrence for analysis. Life history stages of nekton and prey are in parentheses and represent: egg (e), megalopa larva (m), larva (l), juvenile (j), furcilia (f), yearling (y) and adult (a); nekton and prey with no indication of life history stage are adult.

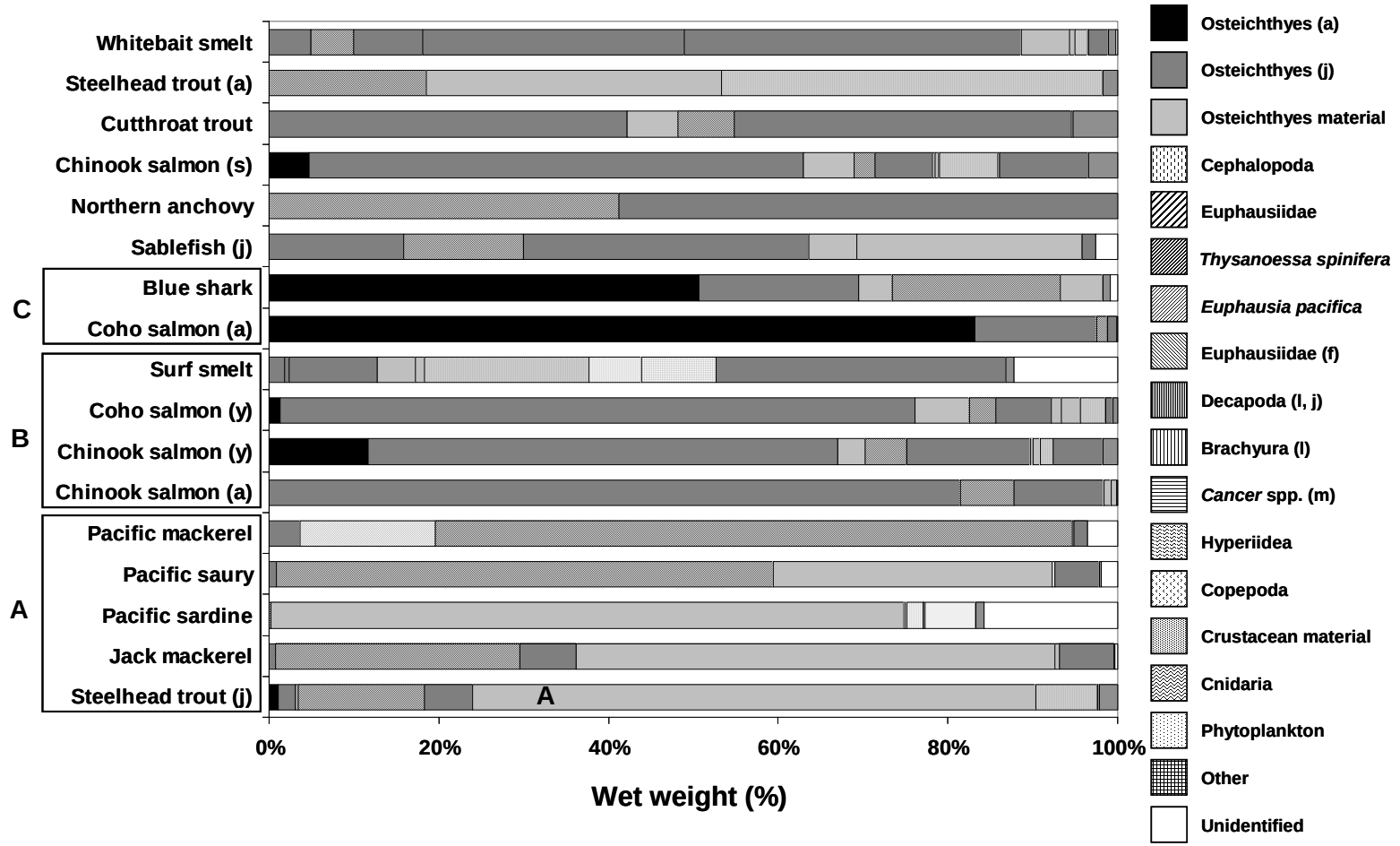

Figure 2.2. August 2000 nekton diets. Groups based on cluster analysis of diets (% wet weight) are blocked and labeled by low (A) to higher (C) trophic groups. Species not blocked lacked sufficient numbers and frequency of occurrence for analysis. Life history stages of nekton and prey are in parentheses and represent: egg (e), megalopa larva (m), larva (l), juvenile (j), furcilia (f), yearling (y) and adult (a); nekton and prey with no indication of life history stage are adult.

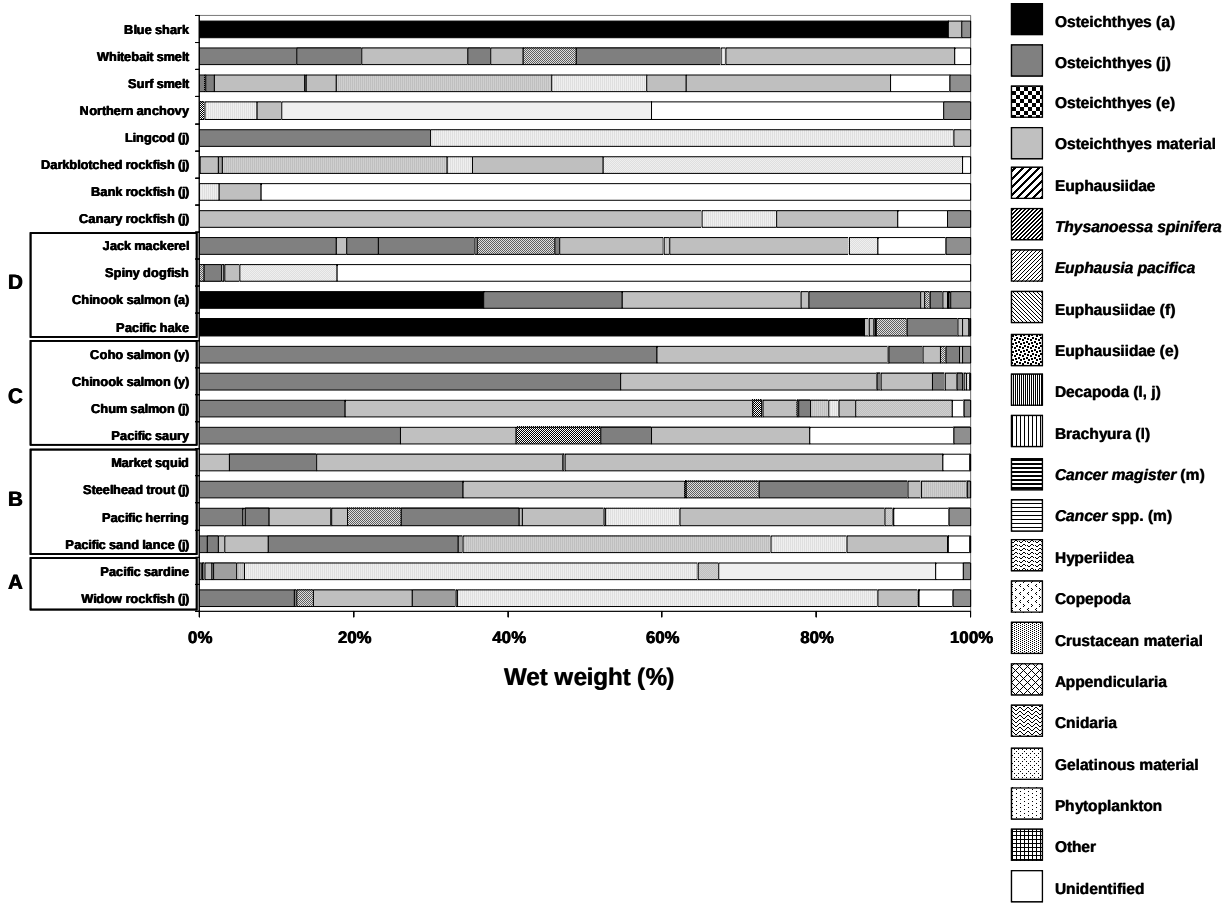

Figure 2.3. June 2002 nekton diets. Groups based on cluster analysis of diets (% wet weight) are blocked and labeled by low (A) to higher (D) trophic groups. Species not blocked lacked sufficient numbers and frequency of occurrence for analysis. Life history stages of nekton and prey are in parentheses and represent: egg (e), megalopa larva (m), larva (l), juvenile (j), furcilia (f), yearling (y) and adult (a); nekton and prey with no indication of life history stage are adult.

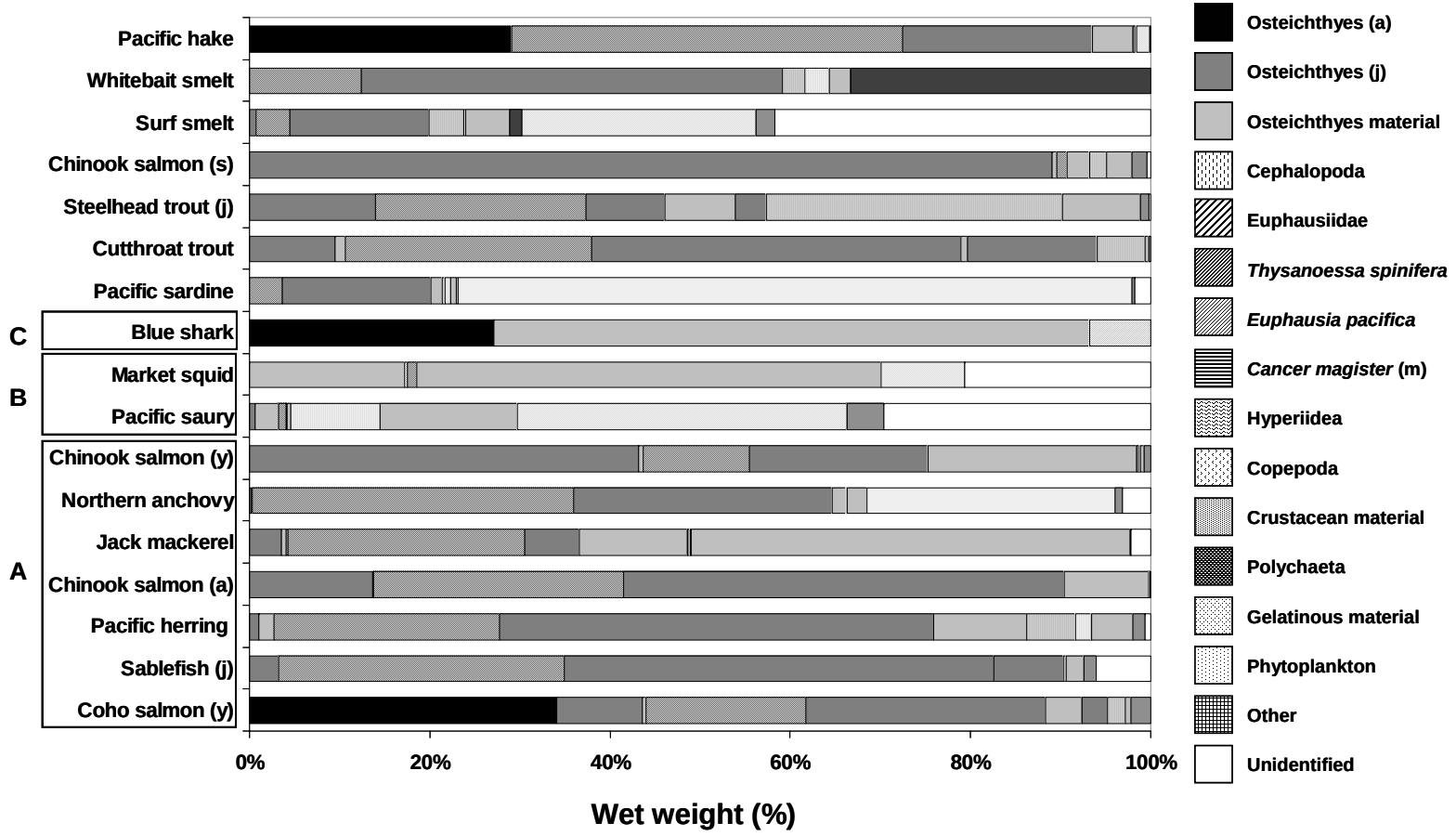

Figure 2.4. August 2002 nekton diets. Groups based on cluster analysis of diets (% wet weight) are blocked and labeled by low (A) to higher (C) trophic groups. Species not blocked lacked sufficient numbers and frequency of occurrence for analysis Life history stages of nekton and prey are in parentheses and represent: megalopa larva (m), juvenile (j), yearling (y) and adult (a); nekton and prey with no indication of life history stage are adult.

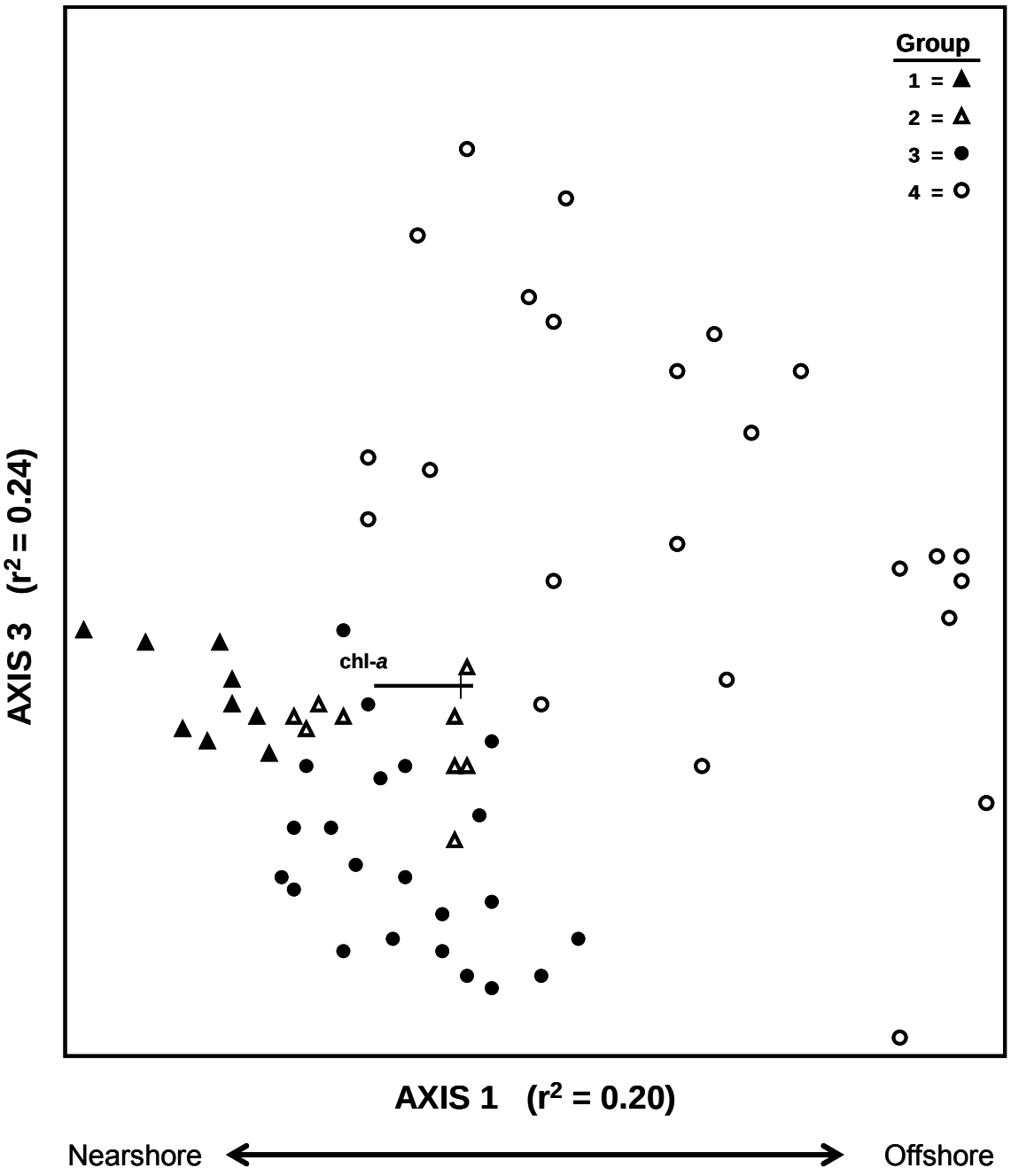

Figure 2.5. June 2000 Non-metric multidimensional scaling (NMS) joint plot (stress 15.8, final instability = 0.0002, 500 iterations) of predator-station by prey species matrix of percent wet weight contribution to diet. Groups 1-4 were derived from cluster analysis.

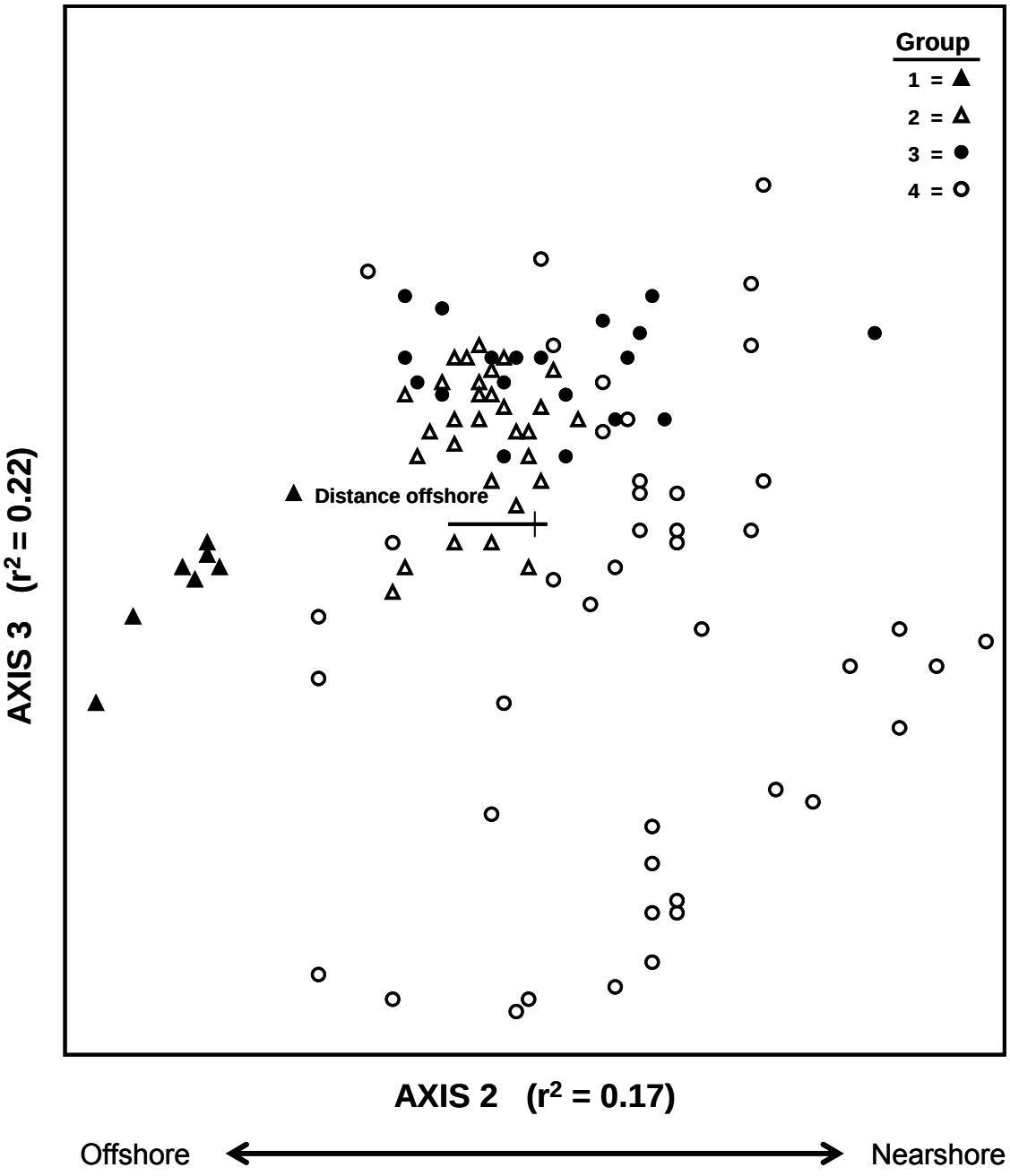

Figure 2.6. August 2000 Non-metric multidimensional scaling (NMS) joint plot (stress = 16.9, final instability << 0.0001, 229 iterations) of predator-station by prey species matrix of percent wet weight contribution to diet. Groups 1-4 were derived from cluster analysis.

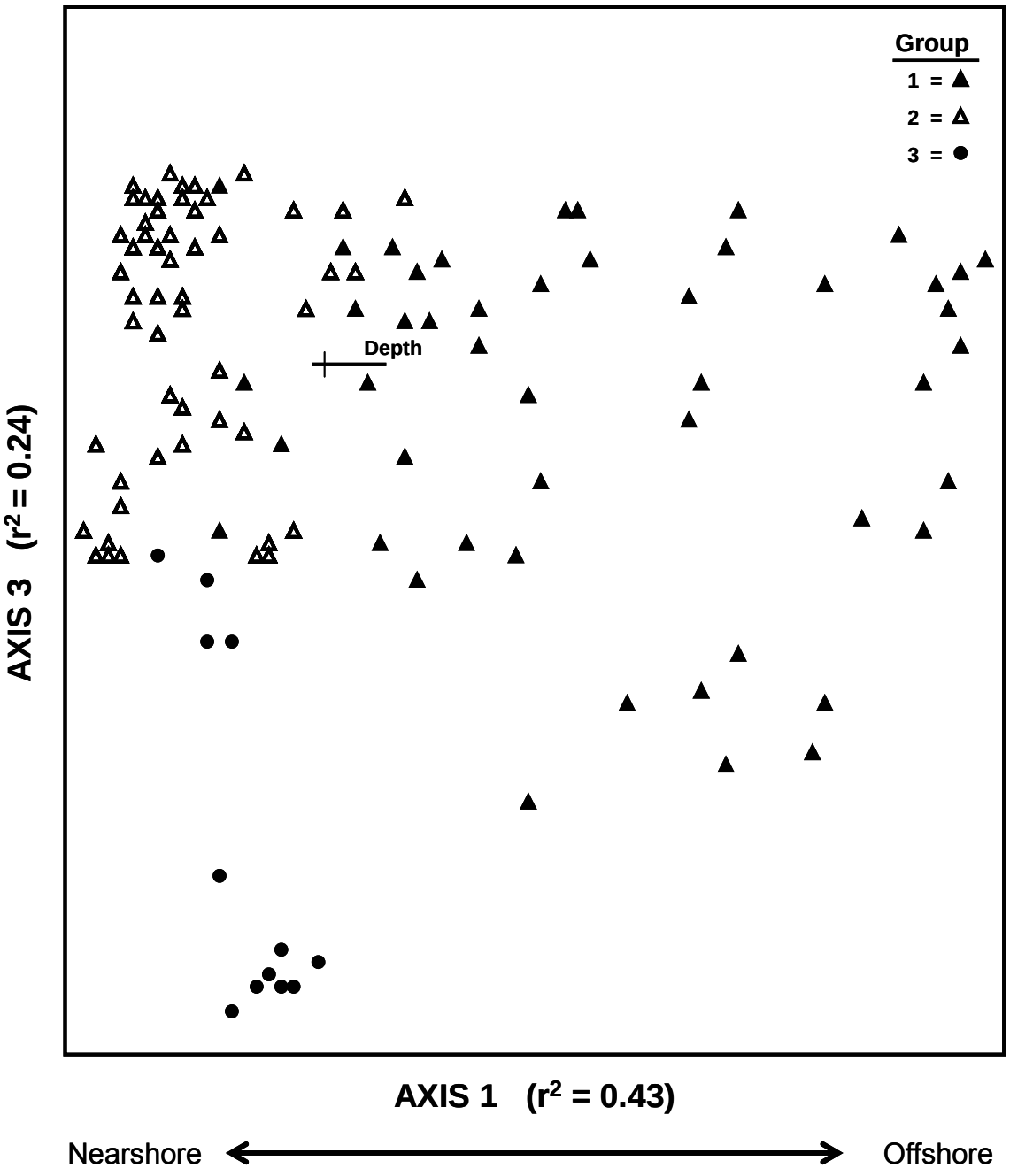

Figure 2.7. June 2002 Non-metric multidimensional scaling (NMS) joint plot (stress = 15.8, final instability = 0.001, 500 iterations) of predator-station by prey species matrix of percent wet weight contribution to diet. Groups 1-4 were derived from cluster analysis.

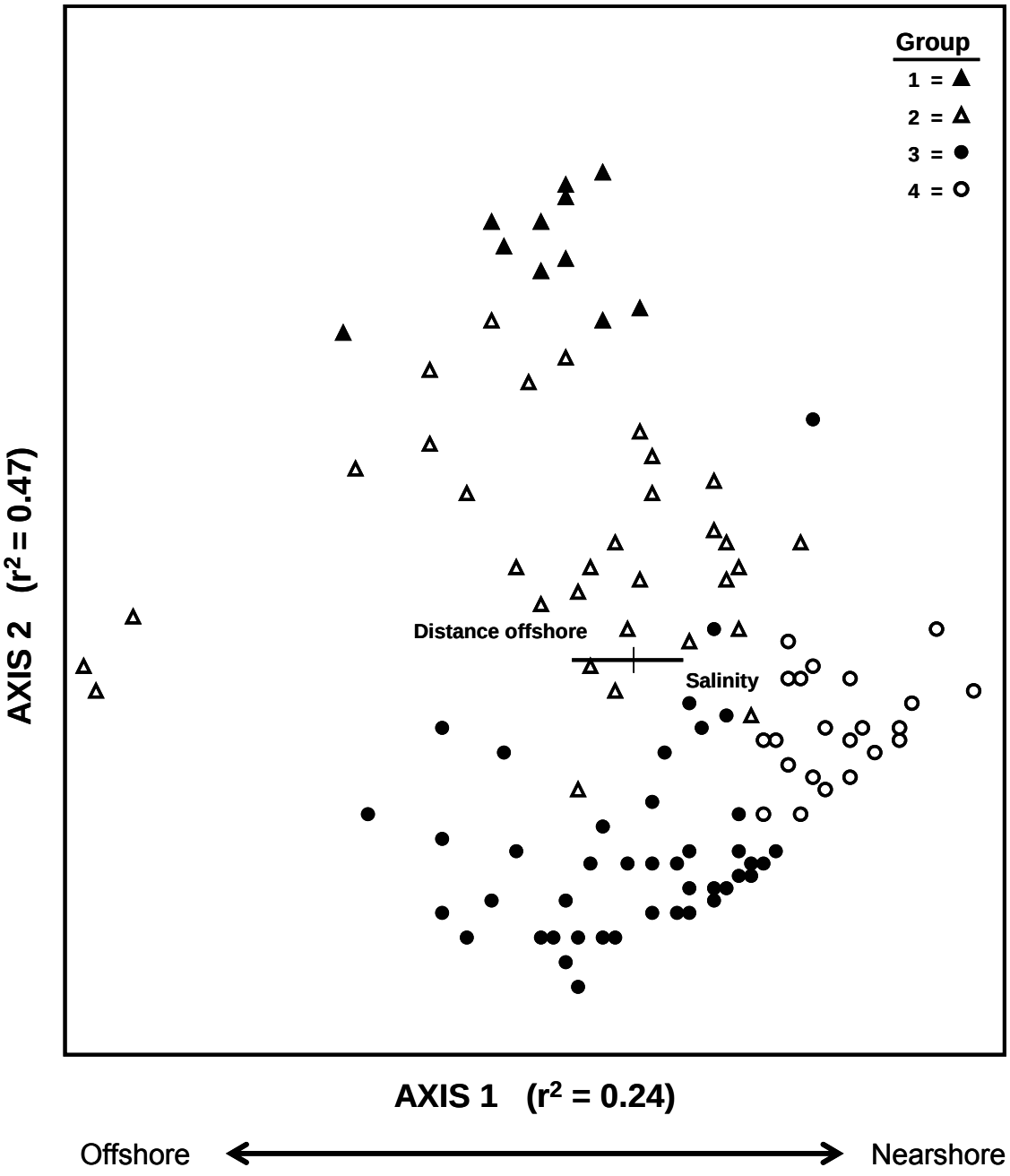

Figure 2.8. August 2002 Non-metric multidimensional scaling (NMS) joint plot (stress = 13.9, final instability = 0.005, 500 iterations) of predator-station by prey species matrix of percent wet weight contribution to diet. Groups 1-4 were derived from cluster analysis.

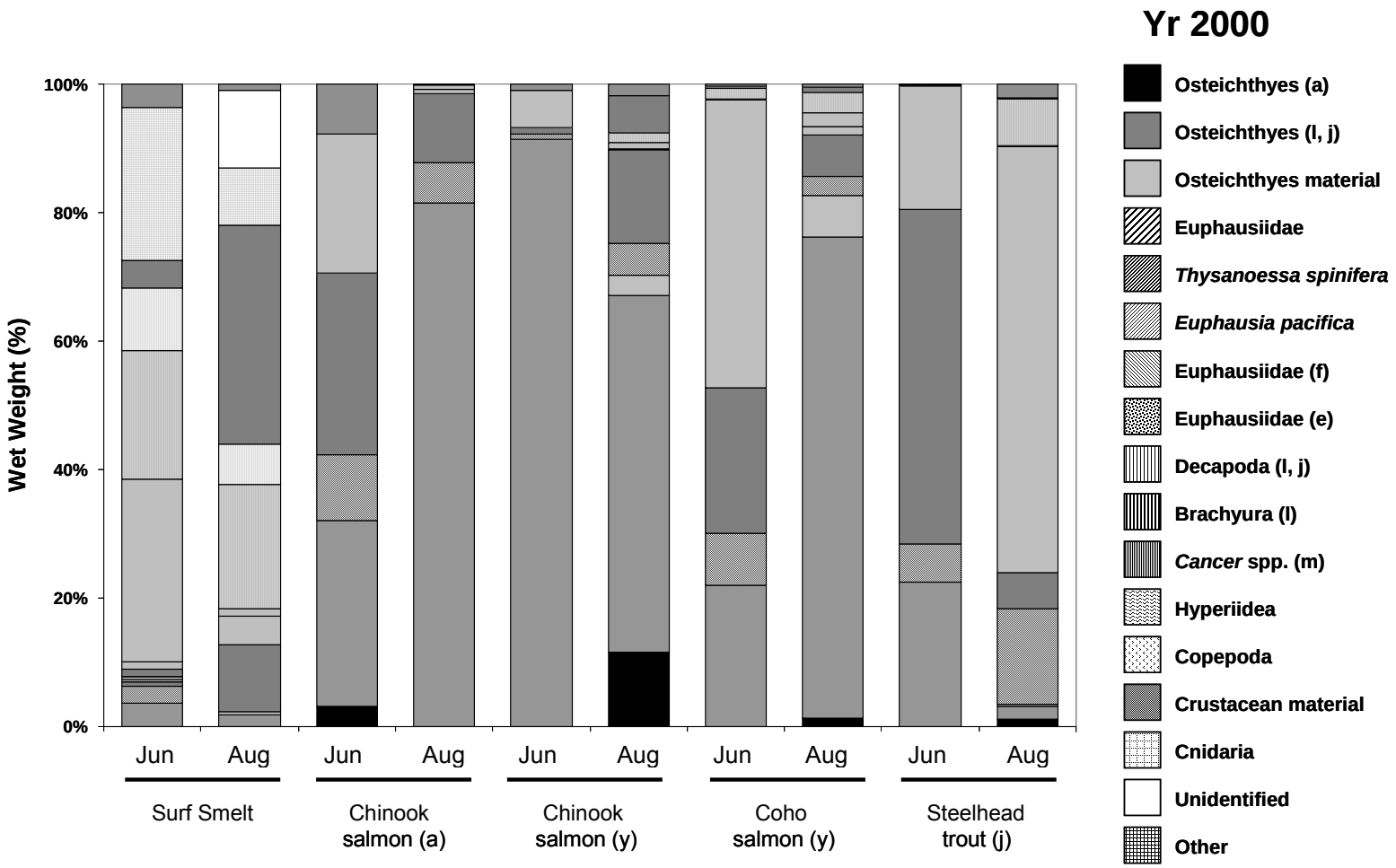

Figure 2.9. Comparison of June (Jun) and August (Aug) 2000 nekton diets (percent wet weight). Life history stages are noted in parentheses as: larva (l), megalopa larva (m), juvenile (j), furcilia (f), yearling (y), and adult (a).

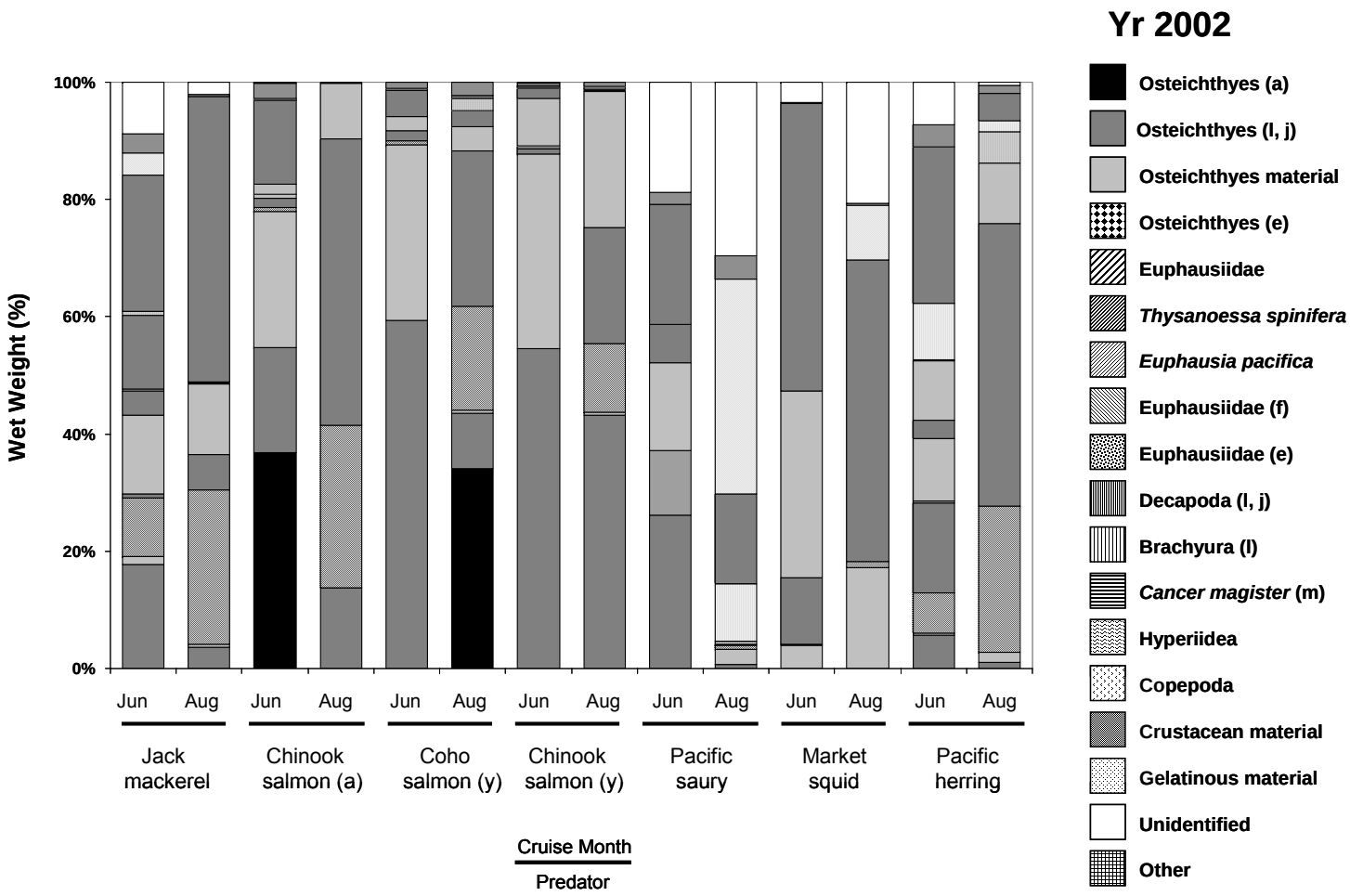

Figure 2.10. Comparison of June (Jun) and August (Aug) 2002 nekton diets (percent wet weight). Nekton life history stages are adult unless noted in parentheses as: yearling (y), and adult (a) for Chinook salmon.

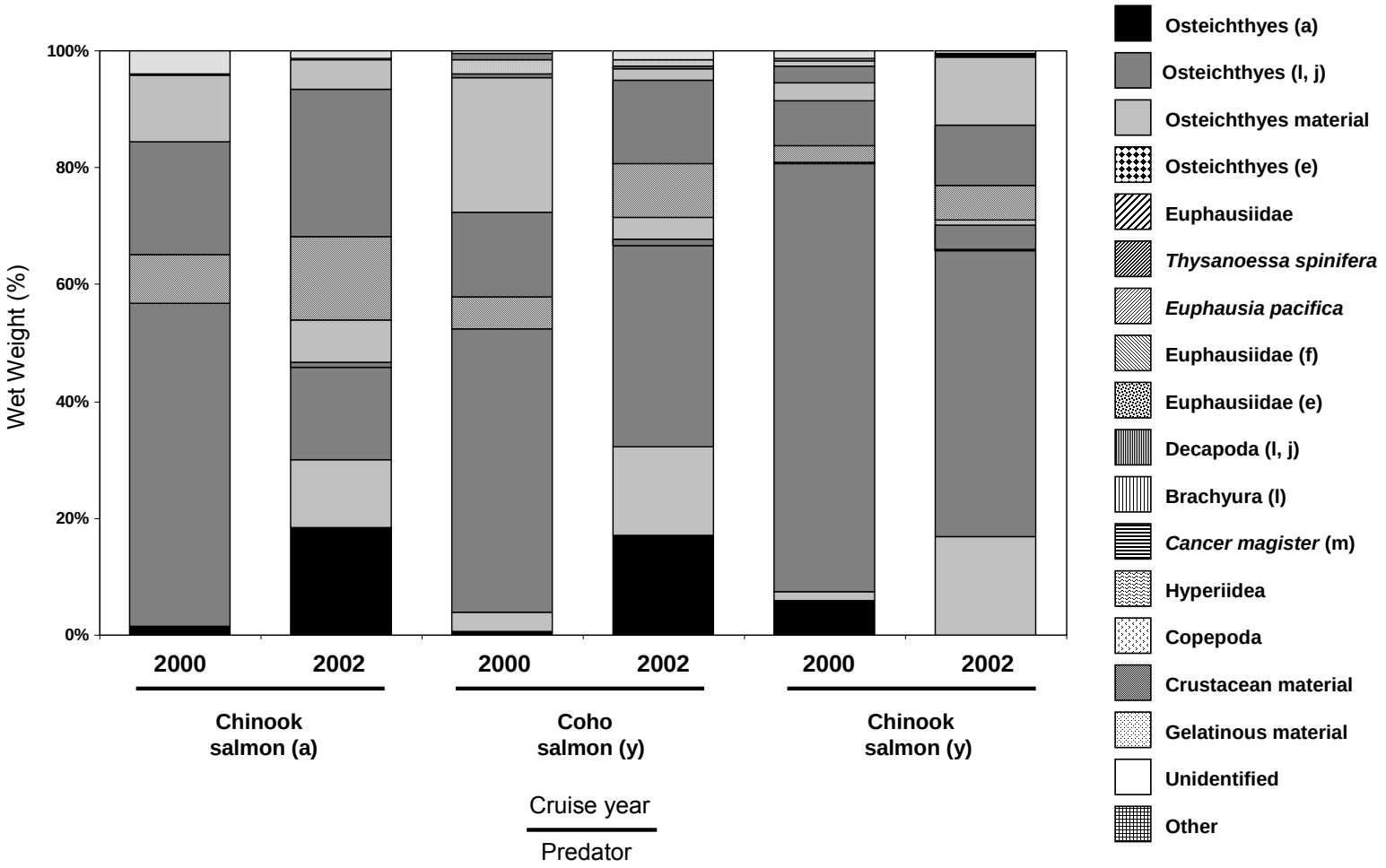

Figure 2.11. Comparison of 2000 and 2002 nekton diets (percent wet weight). Nekton life history stages are denoted in parentheses as: yearling (y) and adult (a).

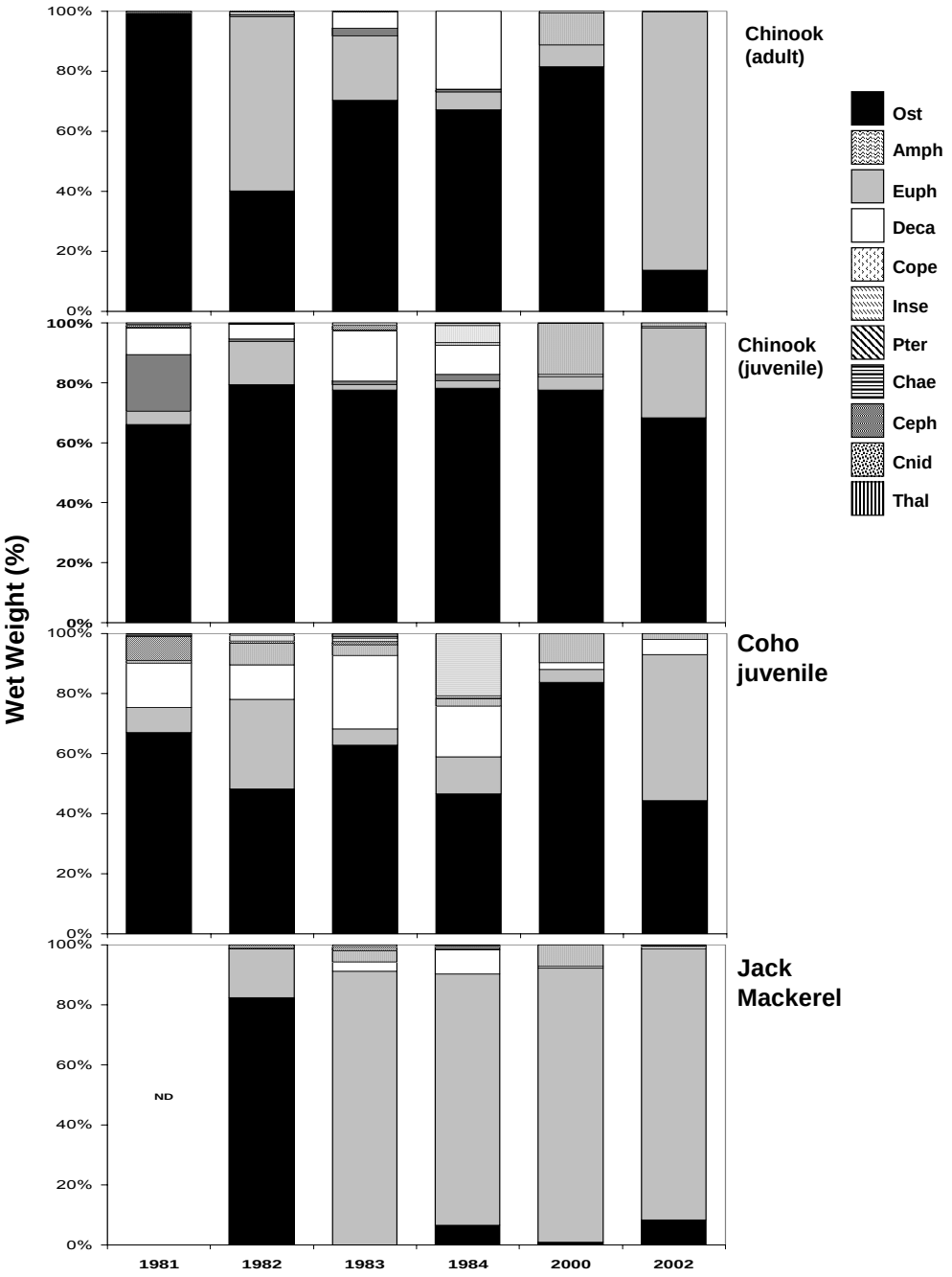

Figure 2.12. Comparison of nekton diets (percent wet weight) by year. Years 1981-1984 data are from Brodeur and Pearcy (1992) and 2000 and 2002 from this study. Years with no data are denoted as ND. Nekton life history stages are adults unless noted in parentheses as: juvenile (j) and adult (a) for Chinook salmon. Nekton prey are abbreviated as the following: Osteichthyes (Ost), Amphipoda (Amph), euphausiidae (Euph), Decapoda (Deca), Copepoda (Cope), Insecta (inse), Pteropoda (Pter), Chaetognatha (Chae), Cephalopoda (Ceph), Cnidaria (Cnid), and Thaliacia (Thal).

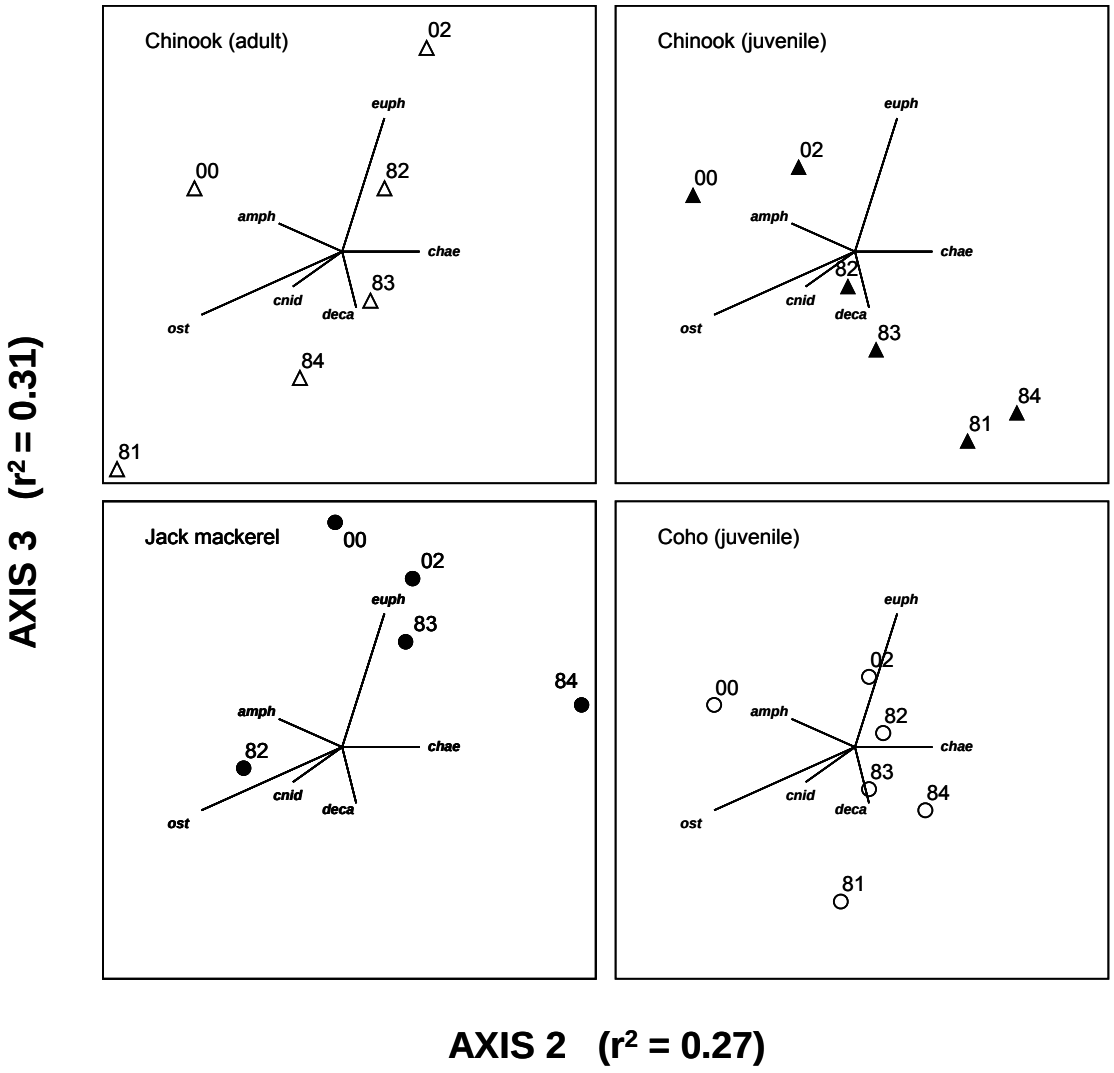

Figure 2.13. Non-metric multidimentional scaling (NMS) joint plots of nekton diets from July-August 1981-1984 (Brodeur and Pearcy 1992) and July-August 2000 and 2002 cruises. Joint plots are from a single NMS joint plot (stress = 15.9, final instability = 0.0007, 500 iterations), divided by nekton species to allow easier comparison among years. Individual joints denote prey with correlation coefficients with r^2 values of $\geq$0.2, and are abbreviated as the following: Osteichthyes (ost), Amphipoda (amph), Copepoda (cope), Decapoda (deca), Cnidaria (cnid), Chaetognatha (chae) and Euphausiidae (euph).

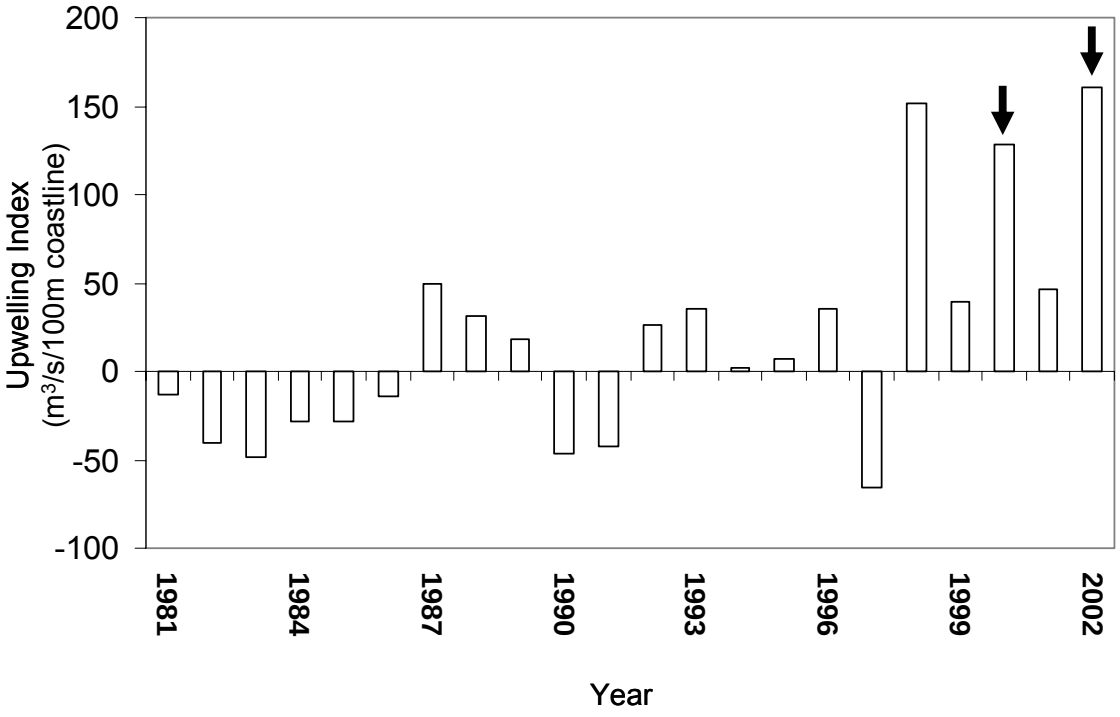

Figure 2.14. Yearly (mean) upwelling anomalies from 45 deg latitude. Nekton diets were analyzed during high upwelling years of June/August 2000 and 2002 (arrows). Data were obtained from the National Oceanic Atmospheric Administration (NOAA) Pacific Fisheries Environmental Laboratory (PFEL)(http://www.pfeg.noaa.gov/products).

CHAPTER 3

TROPHIC DYNAMICS OF ZOOPLANKTON AND NEKTON IN THE NORTHERN CALIFORNIA CURRENT ECOSYSTEM – AN INTEGRATED APPROACH TO USING DIET AND STABLE ISOTOPE ANALYSES

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ABSTRACT

Food web studies typically rely on direct observation of diets or application of stable isotopes, but rarely both. In this study we examined the trophic relationships of dominant marine nekton and zooplankton within the Northern California Current (NCC) ecosystem using a combination of diet analyses and carbon and nitrogen stable isotopes. Samples of nekton and zooplankton were collected in June and August 2000 and 2002 research cruises off the shelf-slope of Northern California to central Oregon. Diet analyses revealed major trophic groups that generally coincided with increasing $\delta^{15}N$ during the end of seasonal production, however considerable dietary overlap among adjacent trophic groups obscured absolute distinctions. The NCC appears to consist of four trophic levels between particulate organic matter and the highest trophic level, with mean trophic level fractionation of 3.0‰ for $\delta^{15}N$ and between 0-0.7‰ for $\delta^{13}C$. Much of overlap between trophic groups was due to the consumption of euphausiids and larval-juvenile fishes. The combined use of stable isotopes and diet analyses therefore provided considerable insight into the trophic relationships within this system. For nearly all species of nekton and zooplankton, there was a seasonal increase in $\delta^{13}C$ and $\delta^{15}N$ between June and August for both years, indicating the importance of considering temporal integration of stable isotopes in ecosystems with seasonal production. We also observed considerable variation in $\delta^{13}C$ that coincided with nearshore-offshore distributions of some species of nekton and some zooplankton, providing a biogeochemical marker to delineate onshore and offshore communities.

INTRODUCTION

Understanding trophic relationships within an ecosystem is essential for recognizing the biotic and abiotic (e.g. upwelling) factors, which may drive ecosystem stability and persistence (McCann 2000). Large marine ecosystems such as eastern boundary current upwelling zones contribute to ~20% of world fish production (Mann 2000), yet surprisingly little empirical data is available on the trophic relationships within these

ecosystems. Most trophic analyses within these systems have traditionally focused on only a few dominant species based on diet analyses (e.g., hake – Tanasichuk 2002; sardine – Van Der Lingen 2002; horse mackerel – Pillar and Wilkinson 1995). Recently, stable isotopes have become a common tool in ecology to elucidate trophic patterns (Rau et al. 1992, Hobson et al. 1994, Sherwood and Rose 2005), migration (Fry 1981, Hesslein et al. 1991, Hansson et al. 1997) and source production (Haines and Montague 1979, Hobson et al. 1994, Perry et al. 1999). Still, applications of stable isotopes in marine food webs have only focused mainly on zooplankton (e.g. Wu et al. 1997) or only a subset of taxa (e.g. Sholto-Douglas et al. 1991, Monteiro et al. 1991, Perry et al 1999, Bode et al. 2003) from major upwelling zones. Advances in ecological modeling (e.g. Ecopath, Ecosim) have increased model application to large marine ecosystems and associated species and complexity (Christiansen and Walters 2004). A major limitation to these models has been the scarcity of detailed empirical data to accurately represent the trophic interactions with the ecosystems examined.

Measuring trophic relationships or connectivity is problematic due to the complexities inherent in ecological systems. However, conventional analyses of dietary composition provide a base knowledge for understanding these relationships. Examination of diets using stomach content analysis can provide very detailed information of an organism's feeding behavior, including the number and size of prey species, and total amount of food consumed. A major limitation of stomach content analyses is it only provides a recent "picture" of feeding and fails to capture the longer-term aspects of trophic behavior.

Alternatively, within the last several decades, stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) have become a common tool in elucidating relative trophic position and source of base production of an organism (for reviews see Michener and Schell 1994, Post 2002). Stable isotopes are based on the differential uptake of the heavier isotope (^{15}N and ^{13}C) over the lighter (^{14}N and ^{12}C) in diet over time, representing a time-averaged signature of its assimilated diet (Tieszen et al. 1983, Peterson and Fry 1987,

Post 2002). For nitrogen, a predator preferentially retains the heavier (^{15}N) isotope over the lighter (^{14}N) of its diet, with each trophic level accounting for an approximate enrichment of 3.4 ‰ relative to its prey (Post 2002). This trophic level enrichment, termed 'fractionation', is a result of the differential retention of a particular stable isotope within an element over another (Tieszen et al. 1983), also expressed as $\Delta\delta^{15}N$ (or ^{13}C) = $\delta^{15}N_{consumer} - \delta^{15}N_{base}$, where $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value of the consumer and $\delta^{15}N_{base}$ is that of its food source. For carbon stable isotopes (^{13}C and ^{12}C), trophic fractionation is less pronounced between trophic levels (0.4 ‰, Post 2002) allowing for it to be used as a tracer of source primary production (Hobson 1999). A major shortcoming of stable isotopes is that they lack the descriptive and quantitative results provided through diet analyses, a fundamental component in accurately describing food webs. Ideally a method of using both diet and stable isotopes can provide a more in-depth measure of determining trophic relationships because they are complimentary in describing specific prey consumed while measuring assimilated diet over time (Tieszen et al. 1983).

One of four major eastern boundary current upwelling ecosystems of the world, the California Current (CC) is highly productive and is associated with an abundance of sardine, anchovy, mackerel and hake species (Brodeur and Pearcy 1986, Brodeur et al. 2003, 2005). The northern region of this system, termed the Northern California Current (NCC) ecosystem, resides between Cape Mendocino, California (Lat. 40° 10') and southern Vancouver Island, British Columbia (Lat. 49° 11' N). During spring and summer months (May-September), strong and persistent coastal upwelling provides nutrient-rich water to fuel surface primary production (Hood et al. 1991, Sackman et al. 2004). Interannual fluctuations in upwelling intensity, particularly between El Niño and La Niña years, have been strongly associated with changes in primary production (Corwith and Wheeler 2002, Thomas et al. 2003), zooplankton (Miller et al. 1985, Peterson et al. 2002, Peterson and Keister 2002), and higher trophic levels (Pearcy and

Schoener 1987, Pearcy 2002, Brodeur et al. 2005). Lower-frequency, interdecadal scale processes, such as shifts in the Pacific Decadal Oscillation (PDO, Mantua et al. 1997), are also associated with changes in upwelling and zooplankton biomass (Roemmich and McGowan 1995, Brodeur et al. 1996) and nekton community composition (McGowan et al. 1998, Emmett and Brodeur 2000).

Since the late 1990s the NCC has exhibited a general shift in the PDO that may be associated with a shift to a more productive 'cool' regime (Peterson and Schwing 2003). Significant changes in NCC nekton community have occurred with sardines becoming one of the most abundant nekton species (Emmett and Brodeur 2000, Emmett et al. 2005) after an absence of almost 50 years. The NCC system has also exhibited a coastal hypoxic "dead" zone (Grantham et al. 2004), associated with advection of cool, nutrient-rich subarctic water in 2002 (Wheeler et al. 2003). The observed correlation of abiotic factors and a biotic response in the NCC clearly indicates the importance of abiotic environmental effects on ecosystem functioning.

There are currently many gaps in our understanding of trophic relationships that reside in the NCC system and the biotic response to changes in abiotic forcing such as upwelling intensity. Knowledge of trophic relationships can also help deduce the importance of competition and predation that may shape populations and recruitment, essential parameters for fisheries recruitment and ecological models. Using both stable isotopes and diet analyses can elucidate patterns that would otherwise not be revealed individually (Hicks 1997). If stable isotopes are a measure of past relative trophic position and source production, then we would predict some coherence between trophic level patterns in stable isotopes of predators and their primary prey. In this study I compared the results from diet and stable isotopes and used both methods to examine the trophic connections

between nekton and zooplankton within the NCC shelf and slope ecosystem. My results provided an in-depth analysis of the trophic relationships between zooplankton and nekton, and revealed the importance of considering temporal (time-lag) and spatial scales in using stable isotopes in a large marine ecosystem.

METHODS

Field Collection

Collections of nekton and most zooplankton for this study occurred from Northeast Pacific Global Ocean Ecosystems Dynamics (GLOBEC) cruises during June and August 2000 and 2002. Sampling occurred along a series of transects across the shelf between Crescent City, California (Lat 41° 54.0') and Newport Oregon (Lat. 44° 39.0') (Brodeur et al. 2004, Reese and Brodeur 2006). At each station nekton were collected using a Nordic-264 rope trawl (30 m wide by 18 m depth) towed for 30 minutes. Macrozooplankton such as gelatinous zooplankton, adult euphausiids and larval-juvenile fish were occasionally retained in the Nordic trawl and were collected for isotope analysis. Smaller zooplankton (<5 mm) were collected using surface neuston hauls (1 m^2 mouth, 335 μm mesh; see Reese et al. 2005 for sampling details). Some zooplankton collections for decapod larvae and copepods were made from June and September 2002 cruises just north of our study region. Particulate organic matter (POM) samples were collected using a Niskin bottle sampled at 3 m depth. Niskin samples were pre-filtered through a 64 μm sieve to remove zooplankton, and then filtered through a 47 mm glass fiber filter (~0.7 μm) at ~10 psi pressure. All nekton, zooplankton and POM samples were immediately frozen on ship (-20ºC) following collection and later taken to the laboratory for processing. At each sampling location, sea surface temperature (3 m), salinity, and chlorophyll-a (chl-*a*) were measured. A detailed description of environmental data collection is provided in Reese and Brodeur (2006).

Laboratory

Laboratory processing of nekton involved measurement of individuals and extraction of tissue for isotope analysis. Diet analysis of nekton from the same collections was performed and has been reported elsewhere (Miller in-prep., Ch 2 this dissertation). Lengths of fish were measured (±1.0 mm) using fork, total, or standard length and market squid (*Loligo opalescens*) were measured using dorsal mantle length. Tissue was then extracted from nekton for stable isotope analysis. For fish, a portion of left anterior-dorsal muscle tissue was removed; for market squid a portion of dorsal mantle was extracted. Tissues were oven dried at 60° C for 36 h. Zooplankton samples were thawed in the lab and sorted for specific species or groups of interest: larval/juvenile fish, adult euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera*), large calanoid copepods (2+ mm prosome length, e.g. *Calanus* and *Metridia*), and small calanoid copepods (0.7-1.0 mm prosome length, primarily *Acartia* spp. and smaller life stages of *Metridia*), crab megalopae (*Cancer oregonensis*/*productus*, *Cancer magister*, *Cancer antennarius*/*gracilis*) and macrozooplankton (>5 mm) were dried using a freeze dryer for 36 h. There is no apparent effect of different drying methods on stable isotope ratios of carbon and nitrogen (Bosley and Wainright 1999). For POM samples, carbon and nitrogen isotope ratios were measured separately within each sample to allow for acid treatment of carbon without affecting the nitrogen signature. A subsample of the filter was taken prior to treatment for analyses of $\delta^{15}N$. Acid treatment of the carbon sample was done by fumigating the POM filter with 12 molar HCL for 24 h. Both carbon and nitrogen samples were dried in a drying oven for 24 h at 60° C. After drying, all samples were pulverized using a mortar and pestle, weighed and sent to one of two labs to measure stable isotope ratios.

Most of the samples were sent to the National Marine Fisheries Service Northwest Fisheries Science Center (Seattle, Washington) isotope laboratory and run on a Costech ECS 4010 elemental analyzer coupled to a Thermo Electron Delta Plus stable isotope ratio mass spectrometer. Precision for the isotope analysis was $< \pm 0.3$ for $\delta^{15}N$ and $< \pm 0.2$

for $\delta^{13}C$. Nitrogen and carbon values were referenced to air and Vienna Pee Dee Belemnite, respectively. Remaining samples were sent to the National Aeronautics and Space Administration (NASA) Ames Research Center (Moffett Field, California) using a Carlo Erba 1108 elemental analyzer coupled to a Finnigan Mat, Delta Plus mass spectrometer; instrument precision for carbon and nitrogen were ±0.08 and ±0.25, respecitively. After analyses, carbon isotopes were lipid-adjusted using an equation devised by McConnaughy and McRoy (1979). Lipids can unduly influence carbon isotope ratios because they have a tendency to retain the lighter carbon isotope (C^{12}) over the heavier (C^{13}) isotope (McConnaughy and McRoy 1979).

Analyses

Differences in $\delta^{13}C$ and $\delta^{15}N$ between closely related species or within a species (e.g. seasonal and interannual comparisons) were performed to describe general temporal and trophic-level patterns in the community. Single comparisons were performed post-hoc using a Students t-test for differences in means ($\alpha = 0.05$), whereas multiple comparisons were done using analysis of variance (ANOVA, $\alpha = 0.05$) and Tukey Honestly Significant Difference (HSD) test. Comparisons were also tested for equal distributions using a Kolmogorov-Smirnov test (K-S); when the equal distribution assumption was violated, I used a Mann-Whitney test for differences in medians.

I related nekton diets to stable isotopes $\delta^{13}C$ and $\delta^{15}N$ by first categorizing nekton into trophic groups using agglomerative hierarchical cluster analysis (AHCA), and then plotting cluster groups with respect to $\delta^{13}C$ and $\delta^{15}N$ (generally termed 'isotope space'). Agglomerative hierarchical cluster analysis was done by forming a predator-prey matrix based on the percent wet weight (by year) contribution of major prey taxa (columns) to predator diet (rows) as determined by Miller (in-prep; Chapter 2). The raw data were then transformed using an arc-sine square root transformation to improve normality in the proportional data (Sokal and Rohlf 1995). The cluster analyses were performed using PcOrd (version 4.1, McCune and Mefford 1999) using a flexible beta linkage method (β

= -0.250) and relative Sørensen (Kulcynski) distance measure. Cluster groups were distinguished by choosing an appropriate cutoff level in the dendrograms based on biological meaning while maintaining a moderate to high percentage of information retained (>40%). Significance of cluster groups were then tested using a Multi-Response Permutation Procedure (MRPP) to test the significance of individual groups as they relate to others by chance (McCune and Grace 2002). This procedure derives a within-group agreement value (termed 'A') that provides a measure of the strength of cohesion within each particular group, and ranges from 0-1 for no agreement to 100 for complete agreement. A measure of ≤0.1 is common for biological systems with values ≥0.3 being considered very high (McCune and Grace 2002). Cluster groupings were described in terms of their ranked dominant prey, defined as the top prey categories contributing to ≥70% of the diet. Cluster groups were then related to $\delta^{13}C$ and $\delta^{15}N$ by plotting the $\delta^{13}C$ and $\delta^{15}N$ values of individual nekton species and categorizing them by their respected trophic cluster group. This provided a picture of feeding behavior in isotope space that could be evaluated in terms of relative trophic position ($\delta^{15}N$) and source production ($\delta^{13}C$).

RESULTS

A total of 31 species of pelagic nekton (larval-adult stages), 11 zooplankton (copepods, euphausiids, hyperiid amphipods, and decapod larvae), and 5 gelatinous zooplankton (1 hydrozoan, 3 scyphozoans, 1 ctenophore) taxa were analyzed for $\delta^{13}C$ and $\delta^{15}N$ (Tables 3.1 and 3.2). General trends in $\delta^{15}N$ showed a trophic-level gradient from POM to zooplankton and higher trophic levels (Figs. 3.1 and 3.2); this trend was weak with increasing $\delta^{13}C$ (linear regression: $\delta^{15}N = 17.7 + 0.30\delta^{13}C$, R-sq = 0.08). Within this relationship POM samples displayed the lowest $\delta^{13}C$ and $\delta^{15}N$ values (mean = -21.9 ±0.52‰ and 6.2 ±0.34‰, respectively), with increasing $\delta^{13}C$ and $\delta^{15}N$ in crustacean, gelatinous zooplankton, and species of nekton (Figs. 3.1 and 3.2). Mean $\delta^{13}C$ and $\delta^{15}N$ values including $\delta^{13}C$' (lipid-corrected) and percent carbon/nitrogen ratios are provided in Tables 3.1 and 3.2.

Table 3.1. Summary results from carbon and nitrogen stable isotope analysis of zooplankton and nekton species collected June and August 2000. Species life histories in parenthesis are denoted as: larvae (l), juvenile (j), subyearling (s), yearling (y) and adult (a).

	JUNE					AUGUST				
Taxa	**n**	**$\delta^{15}N$ Ave. (SE)**	**$\Delta^{13}C$ Ave. (SE)**	**$\delta^{13}C'$ Ave.**	**C/N Ave (SE)**	**n**	**$\delta^{15}N$ Ave. (SE)**	**$\delta^{13}C$ Ave. (SE)**	**$\delta^{13}C'$ Ave.**	**C/N Ave. (SE)**
Crustacea										
Euphausia pacifica	24	9.7 (0.2)	-21.4 (0.1)	-20.0	4.2 (0)					
Thysanoessa spinifera	58	11.2 (0.1)	-20.6 (0.1)	-18.6	4.8 (0.1)					
Mollusca										
Market squid (*Loligo opalescens*)	38	13.2 (0.1)	-19.0 (0.1)	-17.0	4.1 (0.1)					
Osteichthyes										
Chinook salmon (s)						13	13.4 (0.3)	-18.8 (0.2)	-16.5	5.0 (0)
Chinook salmon (y)	1	10.9 (0)	-19.6 (0)	-18.4	4.0 (0)	43	13.9 (0.1)	-17.6 (0.1)	-15.4	5.0 (0)
Chinook salmon (a)	4	13.6(0)	-18.7 (0.3)	-17.7	3.8 (0.1)	9	14.0 (0.1)	-19.6 (0.4)	-17.3	5.0 (0)
Coho salmon (y)	2	10.8 (2.1)	-23.9 (0.2)	-21.1	3.6 (0)	26	14.7 (0.1)	-20.4 (0.2)	-18.2	5.0 (0)
Coho salmon (a)						11	14.3 (0.2)	-21.7 (0.3)	-19.4	5.0 (0)
Pacific sardine						14	12.6 (0.2)	-18.3 (0.2)	-16.9	4.1 (0.1)
Pacific herring	28	12.8 (0.1)	-19.8 (0.1)	-17.7	4.4 (0)					
Northern anchovy						4	13.2 (0.6)	-17.1 (0.2)	-16.1	3.8 (0.2)
Lingcod (j)	2	13.6 (0.2)	-18.2 (0.6)	-18.8	3.9 (0.1)					
Pacific sand lance (j)	1	12.9 (0)	-21.3 (0)	-19.5	4.5 (0)					
Pacific tomcod	2	12.4 (0.1)	-24.4 (0.2)	-18.2	4.8 (0.4)					
Sablefish (j)	9	13.3 (0.3)	-20.9 (0.1)	-20.0	3.7 (0)					
Surf smelt	22	12.8 (0.2)	-18.0 (0.2)	-17.3	3.6 (0)					
Whitebait Smelt	15	12.7 (0.2)	-18.4 (0.3)	-17.4	3.8 (0.1)	21	13.2 (0.2)	-18.1 (0.2)	-17.0	3.9 (0.1)
Pacific mackerel						3	13.9 (0.1)	-19.2 (0.5)	-17.4	4.9 (1.2)

(CONTINUED)

Table 3.1 (CONTINUED). Summary results from carbon and nitrogen stable isotope analysis of zooplankton and nekton species collected June and August 2000. Species life histories in parenthesis are denoted as: larvae (l), juvenile (j), subyearling (s), yearling (y) and adult (a).

	JUNE					AUGUST				
Taxa	**n**	**$\delta^{15}N$ Ave. (SE)**	**$\delta^{13}C$ Ave. (SE)**	**$\delta^{13}C'$ Ave.**	**C/N Ave (SE)**	**n**	**$\delta^{15}N$ Ave. (SE)**	**$\delta^{13}C$ Ave. (SE)**	**$\delta^{13}C'$ Ave.**	**C/N Ave. (SE)**
Jack mackerel	6	13.3 (0.3)	-20.3 (0.2)	-17.0	4.2 (0.1)	3	14.7 (0.3)	-15.4 (0.5)	-17.8	3.9 (0.2)
Blue shark						1	13.8 (0)	-18.1 (0)	-18.8	
Pacific saury						10	12.6 (0.2)	NA	NA	3.8 (0)
Pleuronectidae (l)	6	12.3 (0.4)	-17.8 (0.7)	-22.1	3.8 (0.1)					
Sandsole (l)	1	12.9 (0)	-22.0 (0)	-19.5	5.3 (0)					

Table 3.2. Summary results from carbon and nitrogen stable isotope analysis of zooplankton and nekton species collected June and August 2002. Species life histories in parenthesis are denoted as: larvae (l), megalopa (m), juvenile (j), subyearling (s), yearling (y) and adult (a). $\delta^{13}C'$ denotes lipid-corrected carbon isotope ratios and C/N denotes the percent carbon to nitrogen ratio.

	JUNE					AUGUST				
Taxa	**n**	**$\delta^{15}N$ Ave. (SE)**	**$\delta^{13}C$ Ave. (SE)**	**$\delta^{13}C'$ Ave.**	**C/N Ave (SE)**	**n**	**$\delta^{15}N$ Ave. (SE)**	**$\delta^{13}C$ Ave. (SE)**	**$\delta^{13}C'$ Ave.**	**C/N Ave. (SE)**
POM	3	6.5 (0.2)	-23.0 (0.1)	-21.9	NA	38	5.5 (0.5)	-21.4 (0.4)		
Mollusca										
Market squid	23	12.9 (0.1)	-16.7 (0.1)	-16.0	3.5 (0)	18	12.6 (0.1)	-16.1 (0.1)	-15.6	3.5 (NA)
Crustacea										
*Acartia**	11	9.3 (0.2)	-10.0 (0.4)	-10.7	5.4 (0.2)					
*Calanus**	10	8.8 (0.3)	-10.7 (0.1)	-10.7	6.2 (0.5)	5	8.7 (0.3)	-21.7 (0.3)	-16.1	17.6 (1.0)
Copepoda, bulk*	5	9.8 (0.5)	-18.5 (0.8)	-18.6	6.6 (0.2)	17	9.1 (0.1)	-20.6 (0.4)	-16.9	9.5 (1.9)
Copepoda, large* (>1.5 mm PL)	7	10.1 (0.3)	-13.9 (0.3)	-11.3	8.2 (0.6)					
Copepoda, small* (<1.5 mm PL)	4	9.1 (0.2)	ND	ND	6.6 (0.3)					
*Cancer antennarius/gracilis** (m)	15	9.4 (0.2)	-18.9 (0.5)	-18.9	5.5 (0.1)					
*Cancer magister** (m)	32	9.4 (0.2)	-15.0 (0.3)	-15.0	5.4 (0.1)					
*Cancer oregonensis/productus** (m)	45	9.6 (0.1)	-16.6 (0.2)	-16.6	5.5 (0.1)					
Euphausia pacifica						11	9.1 (0.2)	-19.4 (0.3)	-17.9	4.1 (0.1)
Thysanoessa spinifera						21	10.1 (0.1)	-18.6 (0.3)	-16.9	5.3 (0.2)
Themisto pacifica						1	8.5 (0)	-20.9 (0)	-17.9	-
Hyperoche medusarum						4	7.9 (0.2)	-20.1 (0.5)	-17.2	6.1 (0.5)
Gelatinous zooplankton										
Beroe sp.	9	13.3 (0.1)	-17.8 (0.2)	-17.8	NA					
Aequorea sp.	21	11.7 (0.1)	-16.2 (0.5)	-15.9	2.9 (NA)	12	11.6 (2)	-15.1 (1.2)	-16.4	2.9 (0.2)
Aurelia aurita	4	10.8 (0.1)	-18.7 (1.6)	-18.7	NA	15	9.0 (1.2)	-19.1 (0.7)	-17.8	4.0 (0.2)
Chrysaora fuscescens	19	10.2 (1.0)	-15.8 (0.8)	-16.4	3.3 (0.1)	6	10.8 (0.2)	-15.0 (0.2)	NA	NA
Phacellophora camtschatica	8	11.3 (0.3)	-16.1 (0.6)	-16.1	NA	2	12.5 (1.0)	-16.4 (0.8)	NA	NA

(CONTINUED)

Table 3.2 (CONTINUED). Summary results from carbon and nitrogen stable isotope analysis of zooplankton and nekton species collected June and August 2002. Species life histories in parenthesis are denoted as: larvae (l), megalopa (m), juvenile (j), subyearling (s), yearling (y) and adult (a). $\delta^{13}C'$ denotes lipid-corrected carbon isotope ratios and C/N denotes the percent carbon to nitrogen ratio.

	JUNE					AUGUST				
Taxa	**n**	**$\delta^{15}N$ Ave. (SE)**	**$\Delta^{13}C$ Ave. (SE)**	**$\delta^{13}C'$ Ave.**	**C/N Ave (SE)**	**n**	**$\delta^{15}N$ Ave. (SE)**	**$\delta^{13}C$ Ave. (SE)**	**$\delta^{13}C'$ Ave.**	**C/N Ave. (SE)**
Osteichthyes										
Chinook salmon (s)						7	13.7 (0.3)	-18.8 (0.6)	-17.9	3.8 (0.1)
Chinook salmon (y)	5	14.2 (0.2)	-19.8 (0.1)	-16.7	6.7 (0.8)	27	14.5 (0.1)	-18.3 (0.3)	-16.1	5.1 (0.2)
Chinook salmon (a)	17	14.4 (0.1)	-17.8 (0.2)	-16.5	4.3 (0.3)	30	14.2 (0.1)	-20.1 (0.1)	-16.4	7.8 (0.3)
Chum salmon (a)	2	12.6 (0.4)	-21.5 (0.2)	-19.5	4.8 (0.9)					
Chum salmon (j)						1	15.1 (0)	-17.1 (0)	-15.4	4.4(0)
Coho salmon (y)	7	9.6 (0.6)	-21.5 (2.1)	-20.7	3.7 (0.1)	33	14.4 (0.1)	-19.8 (0.3)	-16.9	6.4 (0.4)
Coho salmon (a)	8	13.5 (0.3)	-20.3 (0.2)	-19.4	3.9 (0.4)					
Cutthroat trout						8	14.6 (0.2)	-21.2 (0.2)	-17.7	7.3 (0.4)
Steelhead trout (j)						4	13.4 (0.4)	-19.3 (0.5)	-16.6	5.8 (0.6)
Northern anchovy	5	12.5 (0.1)	-16.5 (0.1)	-16.5	NA	8	13.1 (0.1)	-17.4 (0.1)	-16.6	3.6 (0.6)
Pacific herring	15	13.2 (0.2)	-18.1 (0.1)	-16.3	4.8 (0.3)	25	13.3 (0.1)	-17.5 (0.2)	-16.1	4.3 (0.2)
Pacific sardine	19	12.2 (0.1)	-17.8 (0.1)	-17.3	3.5 (NA)	25	12.3 (0.1)	-20.1 (0.2)	-17.8	5.2 (0.1)
Surf smelt	11	13.1 (0.1)	-17.1 (0)	-16.4	3.6 (NA)	10	13.3 (0.1)	-16.5 (0.1)	-16.3	3.3 (NA)
Whitebait Smelt	15	12.9 (0.3)	-17.3 (0.1)	-16.9	3.4 (NA)	10	13.8 (0.1)	-16.8 (0.1)	NA	NA
Pacific sand lance (j)	33	11.6 (0.1)	-17.6 (0.1)	-17.2	3.5 (NA)					
Pacific hake	6	13.7 (0.1)	-17.2 (0.1)	-17.2	NA					
Jack mackerel	9	14.2 (0.2)	-17.8 (0.3)	-15.7	NA	15	14.5 (0.2)	-18.8 (0.2)	-17.2	4.3 (0.1)
Pacific saury	10	12.4 (0.1)	-20.0 (0.2)	-20.0	NA	21	13.0 (0.1)	-19.0 (0.2)	-17.9	3.5 (NA)
Sablefish (j)						5	13.5 (NA)	-18.0 (0.2)	NA	NA

(CONTINUED)

Table 3.2 (CONTINUED). Summary results from carbon and nitrogen stable isotope analysis of zooplankton and nekton species collected June and August 2002. Species life histories in parenthesis are denoted as: larvae (l), megalopa (m), juvenile (j), subyearling (s), yearling (y) and adult (a). $\delta^{13}C'$ denotes lipid-corrected carbon isotope ratios and C/N denotes the percent carbon to nitrogen ratio.

	JUNE					AUGUST				
Taxa	**n**	**$\delta^{15}N$ Ave. (SE)**	**$\delta^{13}C$ Ave. (SE)**	**$\delta^{13}C'$ Ave.**	**C/N Ave (SE)**	**n**	**$\delta^{15}N$ Ave. (SE)**	**$\delta^{13}C$ Ave. (SE)**	**$\delta^{13}C'$ Ave.**	**C/N Ave. (SE)**
Rex sole (l)	2	11.9 (0.1)	-19.3 (0.1)	-19.3	5.7 (0.4)					
Bank rockfish (j)	2	12.5 (0.1)	-21.7 (0.1)	-21.1	3.5 (0)					
Canary rockfish (j)	3	12.7 (0.1)	-20.8 (0.1)	-20.1	3.5 (0)					
Darkblotched rockfish (j)	4	11.9 (0.2)	-19.6 (0.6)	-19.1	3.4 (0)					
Widow rockfish (j)	15	12.4 (0.1)	-21.6 (0.1)	-21.2	3.5 (0)					
Spiny dogfish	15	12.6 (0.1)	-17.1 (0.1)	-17.5	2.9 (0)					
Blue shark	2	14.5 (0.2)	-18.8 (0)	NA	NA	7	14.7 (0.2)	-17.7 (0.2)	NA	NA
Soupfin shark	1	15.4 (0)	-16.5 (0)	NA	NA					

Zooplankton

Of the crustacean taxa examined, hyperiid amphipods exhibited the lowest $\delta^{15}N$ values (mean = 7.9‰ for *Hyperoche medusarum* and 8.5‰ for *Themisto pacifica*). Copepods, *Cancer* spp. megalopae, and the euphausiid, *E. pacifica*, showed very similar $\delta^{15}N$ values. No significant differences in $\delta^{13}C$ and $\delta^{15}N$ were observed between the copepods *Acartia* and *Calanus*, or bulk copepods (i.e. mixture of 2 or more species and life stages >1.5 mm prosome length) (ANOVA, $p>0.05$). No differences were observed between *Cancer* crab megalopae *C. magister*, *C. oregonensis*/*productus*, and *C. antennarius*/*gracilis* (ANOVA, $p>0.3$, equal variance for $\delta^{13}C$ but unequal for $\delta^{15}N$, Cochran's C test, $p=0.03$). Comparison between the two dominant euphausiid species *E. pacifica* and *T. spinifera* collected in June 2000 and August 2002, showed that *T. spinifera* was significantly higher in $\delta^{13}C$ and $\delta^{15}N$ for both periods (ANOVA, $p<0.05$); mean difference between the two was 1.15 and 1.03‰, respectively.

For gelatinous zooplankton during June 2002, the hydromedusan *Aequorea* sp. and scyphozoan *Chrysaora fuscescens* were significantly different in $\delta^{15}N$ (ANOVA, $p=0.006$), with *Aequorea* on average being 1.5‰ enriched relative to *C. fuscescens*. This difference was not significant by August of the same year (ANOVA, $p=0.16$). No significant difference was observed in $\delta^{13}C$ between the two species during June and August (ANOVA $p=0.77$). Other scyphozoans, *Phacellophora camtschatica* and *Aurelia aurita*, and the ctenophore, *Beroe* sp., were measured for $\delta^{13}C$ and $\delta^{15}N$, but not in sufficient quantity to allow for robust statistical comparisons. The general pattern observed showed *Beroe* to have the highest $\delta^{15}N$ (mean = 13.3±0.09‰), followed by *Aequorea* sp., *P. camtschatica*, *Aurelia aurita*, and *C. fuscescens*. General trends in $\delta^{13}C$ showed *A. aurita* and *Beroe* to be the most negative (mean = -18.7 ±0.62‰ and -17.8±0.22‰, respectively), followed by *C. fuscescens*, and *P. camtschatica*, and *Aequorea*. During August, *P. camtschatica* was most 15N enriched, followed by *Aequorea* sp., *C. fuscescens*, and *Aurelia aurita*. Intraspecific variation in $\delta^{13}C$ and to a lesser extent $\delta^{15}N$ was high in *C. fuscescens*, *Aequorea* sp., and *A. aurita* relative to most

other nekton and zooplankton analyzed (Fig. 3.2). The egg yolk jellyfish, *P. camtschatica* and the ctenophore *Beroe* showed standard errors comparable to other taxa (Table 3.1).

Nekton

Nekton species showed the highest $\delta^{15}N$ values, with the most ^{15}N-enriched being soupfin shark, juvenile chum salmon, cutthroat trout, jack mackerel, and adult Chinook salmon (range of 15.4 – 14.1‰). Species showing mid-range levels of $\delta^{15}N$ were Pacific mackerel, Pacific hake, Pacific herring, and market squid (range = 13.8 – 12.9‰) and lowest $\delta^{15}N$ values were from Pacific sand lance, juvenile rockfish, Pacific sardine, Pacific saury, adult chum salmon and spiny dogfish (range = 12.9 – 11.6‰). Interspecies differences in $\delta^{13}C$ varied widely within groups of similar $\delta^{15}N$ values (Figs. 3.1 and 3.2). In general Pacific saury, juvenile rockfish (all species), rex sole larvae, blue shark, cutthroat trout and adult chum salmon were most depleted in ^{13}C. More mid-level $\delta^{13}C$ species were jack mackerel, Pacific sand lance and spiny dogfish (-17.4 – -17.1‰). Species most enriched in ^{13}C were Pacific herring, whitebait smelt, surf smelt, Pacific sardine and market squid (range = -15.7 – -17.0‰).

Seasonal and Interannual differences

Unequal collections of species occurred between cruises although some species were collected throughout the study to allow for seasonal and interannual comparisons. No significant difference was detected between copepod samples collected during June versus those in August of 2002 for either $\delta^{13}C$ or $\delta^{15}N$ (ANOVA, $p>0.05$). Likewise, no discernable difference was observed between June and August for $\delta^{15}N$; however, August copepods were slightly more enriched in ^{13}C than those collected in June. Nearly all large nektonic species were ^{15}N-enriched in August samples compared to the initial June starting point for both years (Figs. 3.3 and 3.4), the exceptions being *A. aurita*, market squid, whitebait smelt, and adult Chinook salmon during 2002 (Table 3.2). Where sample sizes allowed for statistical comparisons (2002 only), significant seasonal differences in $\delta^{15}N$ were observed in northern anchovy (t-test, $p=0.001$, $n=13$) with $\delta^{15}N$ being higher in

August. Market squid showed the only statistically significant difference between June and August for $\delta^{13}C$ (t-test, p=0.01, n=16), with August squid being more enriched. Remaining nekton species including Chinook salmon, jack mackerel, Pacific herring, Pacific sardine, Pacific saury, whitebait smelt and juvenile sablefish displayed no significant differences in $\delta^{13}C$ or $\delta^{15}N$ between June and August (ANOVA, p>0.05).

In June of 2000 and 2002, $\delta^{13}C$ and $\delta^{15}N$ of yearling coho salmon were highly variable (Fig. 3.1 and 3.2). Outlier analysis (Dixons test**)** from coho salmon grouped by year showed three individuals in 2000 and two in 2002 were significantly different from the remaining yearling coho salmon. For both years, all fish within this outlier group were under 200 mm FL (mean = 163 mm for both). By August (for both years), yearling coho salmon $\delta^{13}C$ and $\delta^{15}N$ values more closely resembled those of the mid-upper fish assemblage (i.e. highest $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 3.1 and 3.2). Interannual differences in within-species $\delta^{13}C$ and $\delta^{15}N$ showed a general pattern of higher $\delta^{15}N$ and $\delta^{13}C$ during 2002 in nekton (Fig. 3.2); however these differences were not wholly consistent and varied by season (month) and by isotope.

Cluster analysis

Agglomerative hierarchical cluster analysis and comparison of cluster group cutoff levels using MRPP resulted in five cluster groups for 2000 and 2002 (MRPP Sorensen distance, within group agreement A=0.45 and 0.27, respectively, Fig. 3.5). Description of individual groups based on the top prey contributing to ≥ 70% of consumers' diet showed a general division from lower to upper trophic levels for both years. The divisions based on primary, secondary and other prey consumed are as follows (denoted as primary/secondary/tertiary prey): a) copepod/euphausiid furcilia/larval fish (mean nekton cluster group $\delta^{13}C$ = -19.48 and $\delta^{15}N$ = 12.91‰); b) euphausiids/mixed prey (e.g., decapod larvae, larval fish, and hyperiid amphipods)(mean nekton cluster group $\delta^{13}C$ = -18.28 and $\delta^{15}N$ = 13.29‰); c) ichthyoplankton/euphausiids (mean nekton cluster group $\delta^{13}C$ = -17.03 and $\delta^{15}N$ = 13.29‰); d) mixed Crustacea (e.g. larval decapods, hyperiid amphipods and copepods) and ichthyoplankton (mean nekton cluster group $\delta^{13}C$ = -17.22

and $\delta^{15}N$ = 13.45‰); and e) adult fish/euphausiids and ichthyoplankton (mean nekton cluster group $\delta^{13}C$ = -18.16 and $\delta^{15}N$ = 14.00‰).

An overlay of diet cluster groups by $\delta^{13}C$ and $\delta^{15}N$ values during June and August of 2000 (Fig. 3.6) and 2002 (Fig. 3.7) showed $\delta^{15}N$ differences related to feeding, although these varied by season and species. During June 2000, the only fish in the copepod feeding group, juvenile lingcod, had nearly the highest $\delta^{15}N$ values in the observed community (mean=13.6‰). June of 2002 contained more species in this group and it generally had $\delta^{15}N$ values as the lowest for nekton species (Fig. 3.7). For June and August of both years, the euphausiid feeding group and mixed crustacean group were very similar in $\delta^{15}N$ but widely dispersed in $\delta^{13}C$. The ichthyoplankton and euphausiid feeding group were highly dispersed in $\delta^{13}C$ and $\delta^{15}N$, primarily due to very low $\delta^{13}C$ (mean = -20.67‰) and $\delta^{15}N$ (mean = 9.60‰) values observed in yearling coho salmon and low $\delta^{15}N$ (mean = 10.87‰) in yearling Chinook salmon (June, Figs. 3.6 and 3.7). These species/life histories more resembled other species within the group by August (Figs. 3.6 and 3.7). Upper trophic level species that consumed adult fish and euphausiids generally expressed the highest $\delta^{15}N$ values (>13.0‰). One notable exception was the placement of market squid in this group during 2002 (primarily due to cannibalism) which was distinctly different in $\delta^{13}C$ and $\delta^{15}N$ from others in the group, and more resembled values from a mixed crustacean feeder.

DISCUSSION

This study provides the first stable isotope and diet analyses of multiple trophic levels within an EBC upwelling system. Other studies have either looked at diet analyses only (e.g., Brodeur and Pearcy 1992), or applied stable isotopes to a very limited number of species and trophic levels (e.g. Bode et al. 2003). Our $\delta^{13}C$ and $\delta^{15}N$ results from nekton resembled those measured by Sydeman et al. (1997) for market squid, juvenile lingcod, juvenile sablefish, Pacific sardine, Chinook salmon and northern anchovy collected near the Farrallon Islands off Northern California. One exception was that Sydeman et al.

(1997) found a higher mean $\delta^{13}C$ value of -17.3‰ (± 0.2) in juvenile sablefish compared to our mean $\delta^{13}C$ of -19.98‰ (± 0.5). Our $\delta^{15}N$ values of POM (mean = 6.0 ±0.5‰) and copepods (mean= 9.3 ±0.2‰) were within the range observed by Wu et al. (1997) for coastal samples of suspended particulate organic matter (SPOM, range= 4.6 – 10.0‰) and zooplankton (range = 6.8 – 11.5‰) off Vancouver Island (British Columbia, Canada). Similarly our $\delta^{13}C$ values of POM, zooplankton and certain larval-juvenile fish matched "shelf" samples by Perry et al. (1999), also off of Vancouver Island. Both Wu et al. (1997) and Perry et al. (1999) observed a strong trend in decreasing $\delta^{15}N$ and $\delta^{13}C$ respectively, from shelf (coastal) to more slope and oceanic water. In seabirds off Northern California, Sydeman et al. (1997) observed higher $\delta^{13}C$ in nearshore foraging species relative to offshore foraging species. In the two dominant euphausiid species we measured, *T. spinifera*, the more inshore species (Gómez-Gutiérrez et al. 2004), was significantly more enriched in $\delta^{13}C$ and $\delta^{15}N$ compared to the more slope-oceanic species *E. pacifica*. Sydeman et al. (1997) examined euphausiids but made no indication which species were analyzed. Furthermore , we observed a similar trend with higher trophic groups; species with more negative (i.e. lower $\delta^{13}C$) values were slope-oceanic oriented species such as blue shark, Pacific saury, and Pacific sardine, whereas nearshore shelf species such as Pacific herring, whitebait and surf smelt, spiny dogfish and market squid (Brodeur et al. 2004, 2005) had higher $\delta^{13}C$. The implications of this difference, particularly related to $\delta^{13}C$, provide a spatial context to trophic position that can partition the NCC into nearshore (shelf) and offshore (slope/oceanic) subsystems (Perry et al. 1999). The general trend of increased $\delta^{13}C$ nearshore relative to offshore has been well-documented in marine (e.g. Kline 1998, Perry et al. 1999, Bode et al. 2004) and freshwater (Keough et al. 1996) ecosystems, and between benthic and pelagic habitats (McConnaughy and McRoy 1979, Thomas and Calhoon 1993, Davenport and Bax 2002, Takai et al. 2004, Vizzini and Mazzola 2005). It would appear that for the NCC system strong coastal upwelling and the presence of upwelling fronts delineate the nearshore from offshore base production which may result in differences in $\delta^{13}C$ and possibly $\delta^{15}N$ (Wu et al. 1997) that transfers up through the food chain. Differences likely arise from differences in base production with respect to a combination of factors including species

composition (e.g., diatoms versus other phytoplankton) and growth (Fry and Wainright 1991), CO_2 (Rau et al. 1997) and nutrient utilization (Wu et al. 1997). Off the shelf-slope of Vancouver Island, Perry et al. (1999) observed differences in $\delta^{13}C$ of POM, zooplankton and larval fish with a shift in the temperature-salinity gradient between shelf and slope/oceanic water masses. Perry et al. (1999) also observed that the higher $\delta^{13}C$ of POM in shelf samples consisted largely of diatoms.

During spring-late summer, our study area including the Northern California to Washington shelf-slope ecosystem exhibits a very well-defined hydrographic delineation between shelf (<150 m depth) and slope-oceanic (>150 m depth) waters. Strong and persistent coastal upwelling brings cool, high salinity, nutrient-rich water to the surface and across the shelf, forming a well-defined upwelling front expressed as a marked shift in sea surface temperature and salinity. This difference is also defined biologically by high nearshore primary production dominated by diatoms, whereas offshore waters were more associated with smaller phytoplankton (e.g. cyanobacteria and photosynthetic eukaryotes) species (Sherr et al. 2005). Nearshore-offshore differences in temperature, growth, species composition and nutrient availability would understandably provide a strong potential for differences in $\delta^{13}C$ at the base of the food web and higher trophic levels.

Dietary analyses indicated the importance of several key prey taxa such as ichthyoplankton, euphausiids, decapod larvae and copepods, but also showed that consumers of these prey were not exclusive to a specific prey category. Euphausiids appeared the most widely consumed taxa across trophic groups. For example, most nekton that consumed ichthyoplankton and/or adult fishes also consumed euphausiids as a secondary prey, and euphausiid feeders often consumed ichthyoplankton as a secondary prey (discussed in Chapter 2). Although nekton consuming primarily ichthyoplankton and/ or adult fishes expressed the highest level of enrichment relative to diet (Figs. 3.3 and 3.4), they were well below the accepted value of 3.4‰ per trophic level fractionation

reviewed in other aquatic studies (Vander Zanden and Rasmussen 2001, Post 2002). Possible reasons for this may be one or a combination of the following: (*i*) fractionation between trophic levels within this system are less than 3.4‰; (*ii*) nekton have not reached isotopic equilibrium with their diet; and/or (*iii*) the observed diet with euphausiids as a secondary prey reduced enrichment of the consumers 'mixture' relative to ichthyoplankton.

Fractionation levels can vary considerably between marine and freshwater ecosystems, trophic levels (fish and invertebrates) and carnivores versus herbivores (Vander Zanden and Rasmussen 2001); it is possible that this may cause some discrepancy between our observed fractionation values and general observations in other studies. As observed in the strong $\delta^{15}N$ shift between June and August in some species (Figs. 3.6 and 3.7) species within this system may not have reached isotopic equilibrium with their diet by August. The NCC ecosystem exhibits extreme seasonal-dependent dominance shifts in zooplankton (Keister and Peterson 2003) and some species of fish are highly migratory (salmonids, mackerels and Pacific hake) causing a continual shift in isotopic equilibrium. Fish have been shown to take from months to years to reach an isotopic equilibrium in diet, which is largely size and growth-dependent (Hesslein et al. 1993, Miller in-press, Chapter 5). Finally, nekton feeding on euphausiids in our study also consumed larval-juvenile fish, and copepod feeders also consumed a mixed diet containing higher trophic levels (primarily euphausiids), potentially obscuring $\delta^{15}N$ values between adjacent trophic groups based on diets, as was observed between all diet-based trophic groups within our study. Sherwood and Rose (2005) estimated mixed effects on cod feeding on a variable and restricted diet, with more variable diets resulting in a lower fractionation factor. Vander Zanden and Rasmussen (1996) asserted that there are often problems associated with defining trophic groups in freshwater pelagic ecosystems where omnivory is prevalent; this was also observed in other stable isotope studies in lakes (Jones and Waldron 2003) and marine ecosystems (Davenport and Bax 2002).

Despite these limitations, there are some general conclusions that can be drawn from the present results. Based on diet analyses, the NCC system appears to consist of four major trophic levels between POM and the upper trophic-level species of fish, which is in agreement with Brodeur and Pearcy's (1992) estimation of four trophic levels from base production to top fish predators. Assuming organisms are somewhat close to isotopic equilibrium by August, estimation of mean trophic fractionation for the food web can be calculated by subtracting the mean $\delta^{15}N$ of POM from the mean $\delta^{15}N$ of top predators and dividing by the number of trophic links (n = 3 links for 4 trophic levels) in this system (Vander Zanden and Rasmussen 2001). For both years (August only), using the mean difference between blue shark (top predator) and POM results in a mean fractionation of 2.5 and 3.0‰ per trophic level for 2000 and 2002, respectively (for August samples only). This fractionation level is a close approximation to the 3.4 ±1.8‰ reviewed by Vander Zanden and Rasmussen (2001).

Measuring trophic fractionation of carbon in our study is more problematic due to the apparent cross-shelf differences in $\delta^{13}C$ through the food web. For some taxa, this may be determined by looking at trophic level differences between species with known nearshore and offshore distributions. Pacific herring and whitebait smelt are more shelf-oriented species (Brodeur et al. 2005) that feed predominantly on adult *T. spinifera* (Miller in-prep; Ch2). Using the mean $\delta^{13}C$ difference between Pacific herring ($\delta^{13}C$ = -16.1‰) and whitebait smelt (mean = -16.8‰) from *T. spinifera* (mean = -16.8‰), we obtain trophic fractionation in $\delta^{13}C$ of 0.0‰ for Pacific herring and 0.7‰ for whitebait smelt. These values are well within the reported trophic fractionations for $\delta^{13}C$ reviewed by Post (2002). We can further extend this to $\delta^{15}N$ using the mean $\delta^{15}N$ values (Table 1). We determined a mean fractionation of 3.2‰ for herring and 3.7‰ for whitebait smelt, which is close to the mean 3.4‰ commonly reported in the literature (Post 2002). However, as with $\delta^{13}C$, $\delta^{15}N$ may vary across the shelf although we did not see any apparent trend in this regard. A more spatially designed sampling effort across the shelf-slope that included conspecifics at lower trophic levels, such as primary consumers, would provide better insight into this pattern.

Our study also occurred during two highly productive years (2000 and 2002) where upwelling intensity was high and the system was in the cool phase of the PDO (Mantua et al. 1997). The NCC system exhibits very strong fluctuations in interannual productivity and species composition, which are often most associated with El Niño and La Niña events, and over greater time scales of interdecadal shifts in production (Peterson and Schwing 2003). Significant insight into the importance of productivity on dietary overlap, particularly with respect to euphausiids, would occur if a similar study were performed during a low-productivity period. Based on Brodeur and Pearcy (1992) observations on differences in food web structure between El Niño and La Niña periods during the 1980s, dietary overlap would decrease during low-productivity years and we would therefore expect isotope ratios of trophic groups or even species to be more separated in isotope space. The importance of this observation is that it confirms the mechanisms by which energy flows through food webs in the advent of high/low productive years from upwelling intensity and persistence, a factor potentially tied to global climate change.

During June of both years some yearling coho and Chinook salmon displayed very different values than expected for consumers of marine ichthyoplankton. For coho yearlings, several outliers had values of $\delta^{13}C$ and $\delta^{15}N$ (mean = -23.14 and 10.4‰, respectively) closely resembled those obtained in freshwater for yearling Coho salmon (mean -25.3 and 8.5, respectively; Chaloner et al. 2002), indicating that these individuals may have recently migrated from their natal streams and still displayed their freshwater isotopic signature (all were <200 mm FL). By August of both years, no indication of stream isotopic signatures was evident and they resembled the remaining upper-level marine nektonic community (Fig. 3.1 and 3.2). This rapid shift could have occurred given the rapid growth exhibited by juvenile salmon between June and August (Brodeur et al. 2004) coupled to high $\delta^{15}N$ uptake by feeding predominantly on larval and juvenile fishes (Fig. 3.3 and 3.4) would likely result in pronounced shift in $\delta^{15}N$ by August. In other species where comparisons could be made, we observed a general seasonal increase in $\delta^{13}C$ and $\delta^{15}N$ from June to August. This increase has been observed in other studies from marine (Wainright and Fry 1994, Rolff 2000, Davenport and Bax 2002, Bode and

Alvarez-Ossorio 2004) and freshwater (Yoshioka et al. 1994, O'Reilly et al. 2002) ecosystems and is probably more associated with shifts in nutrient and growth dynamics at the base of the food web expressed as a temporal increase from spring to summer/late fall. For $\delta^{13}C$ higher diatom production through the summer would reduce CO_2 availability and cause base production to be less isotopically selective. For $\delta^{15}N$ there may be a number of reasons for this seasonal shift including increased recycling of nitrogen within a food web and availability of nitrate in the system (Wu et al. 1997). The NCC system is strongly seasonal and exhibits intense upwelling and productivity that are tied to reproduction and growth in higher trophic levels. The synchrony of seasonal biological activity would understandably provide substantial ^{15}N-enriched inputs to higher trophic levels at certain times of the year which would be expressed in a time-lag of $\delta^{15}N$ to higher trophic levels. For the NCC and similar ecosystems, it is therefore important to consider sampling and time-lag effects to capture the window of productivity (Wainright and Fry 1994) and to consider growth and isotope turnover rates at different trophic levels (O'Reilly et al. 2002).

Several unexpected results from cluster analysis of diet were the placement of market squid into an upper trophic group when it expressed lower $\delta^{15}N$ by cluster analysis, and in the case of juvenile lingcod, cluster analysis placed it in a lower trophic group when it exhibited higher than expected $\delta^{15}N$ values. This may be due in-part to the discrepancy in short term observation of their diets versus long-term average of isotopes. The potential for misplacement can also be higher in omnivores where placement can occur in higher or lower trophic groups (Jepsen and Winemiller 2002). For juvenile lingcod and market squid, their diets showed an ability to feed on lower and upper trophic levels. The high $\delta^{15}N$ level in juvenile lingcod is puzzling because values were as high as blue shark and adult coho salmon which feed more on adult fish. One explanation for this may be due to the high growth rate coupled to high dietary nitrogen in this species and life history stage. In simulations of trophic shifts related to diet in lake trout (*Salvelinus namaycush*), Harvey et al. (2002) observed juvenile lake trout exhibiting rapid growth coupled to a large seasonal increase in $\delta^{15}N$ may result in juvenile fish exhibiting higher $\delta^{15}N$ values

relative to adult conspecifics. We further observed very high $\delta^{15}N$ values in juvenile chum within our study, a life history stage that exhibits rapid growth coupled primarily to a nitrogen-rich diet of ichthyoplankton (~70% wet weight of diet in June 2002 diets, Chapter 2 this Dissertation).

My study only examined POM, meso- and macrozooplankton and the pelagic nekton community and did not include benthic organisms, marine mammals or seabirds as examined by other studies (e.g. Hobson and Welch 1992, Rau et al. 1992, Yoshii et al. 1999, Davenport and Bax 2002, Hobson et al. 2002). POM samples were likely a mixture of the phytoplankton and the microbial food web. Size-fractionation of POM may have helped in further delineating these groups; however, this process is highly labor intensive and is beyond the scope of this study. Examination of isotopic signatures of higher trophic level marine mammals (cetaceans and pinnipeds) and seabirds could add at least another trophic level to this food web, but many birds and marine mammals feed on the same prey as fish, and could possibly show the same lack of trophic distinction observed in this study. Epibenthic and some benthic fish, as well as mesopelagic myctophids that were not analyzed in this study, undoubtedly play an important role in the food web of this region (Bosley et al. 2004).

Stable isotope analysis of gelatinous zooplankton allowed for trophic analysis of an otherwise understudied group in this region, the gelatinous macrozooplankton. Suchman et al. (in review) examined diets of *Chrysaora fuscescens*, *Aurelia labiata* and *Phacellophora camtschatica*, and observed differences among species. *Chrysaora fuscescens* consumed more euphausiid eggs near-shore and consumed more gelatinous taxa offshore; *A. labiata* also generally consumed more euphausiid eggs and *P. camtschatica* consumed more gelatinous taxa where collected. Of the scyphomedusae examined we observed highest $\delta^{15}N$ in *P. camtschatica*, which is in general agreement with Suchman et al. (in review) considering that "gelatinous prey" add another intermediate trophic link between primary consumers (e.g. copepods or krill) and predatory *P. camtschatica*. Likewise, the observation that *C. fuscescens* tends to consume

more gelatinous taxa than *A. labiata* is in general agreement with relative $\delta^{15}N$ levels observed here, with *C. fuscescens* being more enriched than *A. labiata*. Of the gelatinous taxa measured in this study, the ctenophore *Beroe* sp. displayed the highest $\delta^{15}N$ values, comparable to mid-upper trophic level nekton (Fig. 3.2). This taxon has been shown to prey on other ctenophores (Swanberg 1973).

Surprisingly few studies have applied stable isotopes on an ecosystem scale for marine upwelling ecosystems, with most occurring in non-upwelling regions of the world such as the Bering Sea (McConnaughy and McRoy 1979), Tasman Sea, Australia (Davenport and Bax 2002) Northeast Atlantic (Mills et al. 1984, Fry 1988, Sherwood and Rose 2005), Arctic Ocean (Hobson and Welch 1992), and Weddell Sea (Rau et al. 1992) or focusing on only a few select taxa (Monteiro et al. 1991, Sholto-Douglas et al.1991; Bode et al. 2003) . Given the relative importance of EBC systems to fisheries and their apparent susceptibility to abiotic factors and production regimes (Mantua et al. 1997, Chavez et al. 2003) a combination of stable isotopes and diet analysis of major trophic groups can provide useful information on trophic response to abiotic perturbations across basins. Such studies should minimally focus on the dominant nekton (sardine/pilchards, anchovy, hake, and horse mackerel) and zooplankton (copepods, euphausiids and larval fish) during different production regimes and across regional boundaries of an ecosystem.

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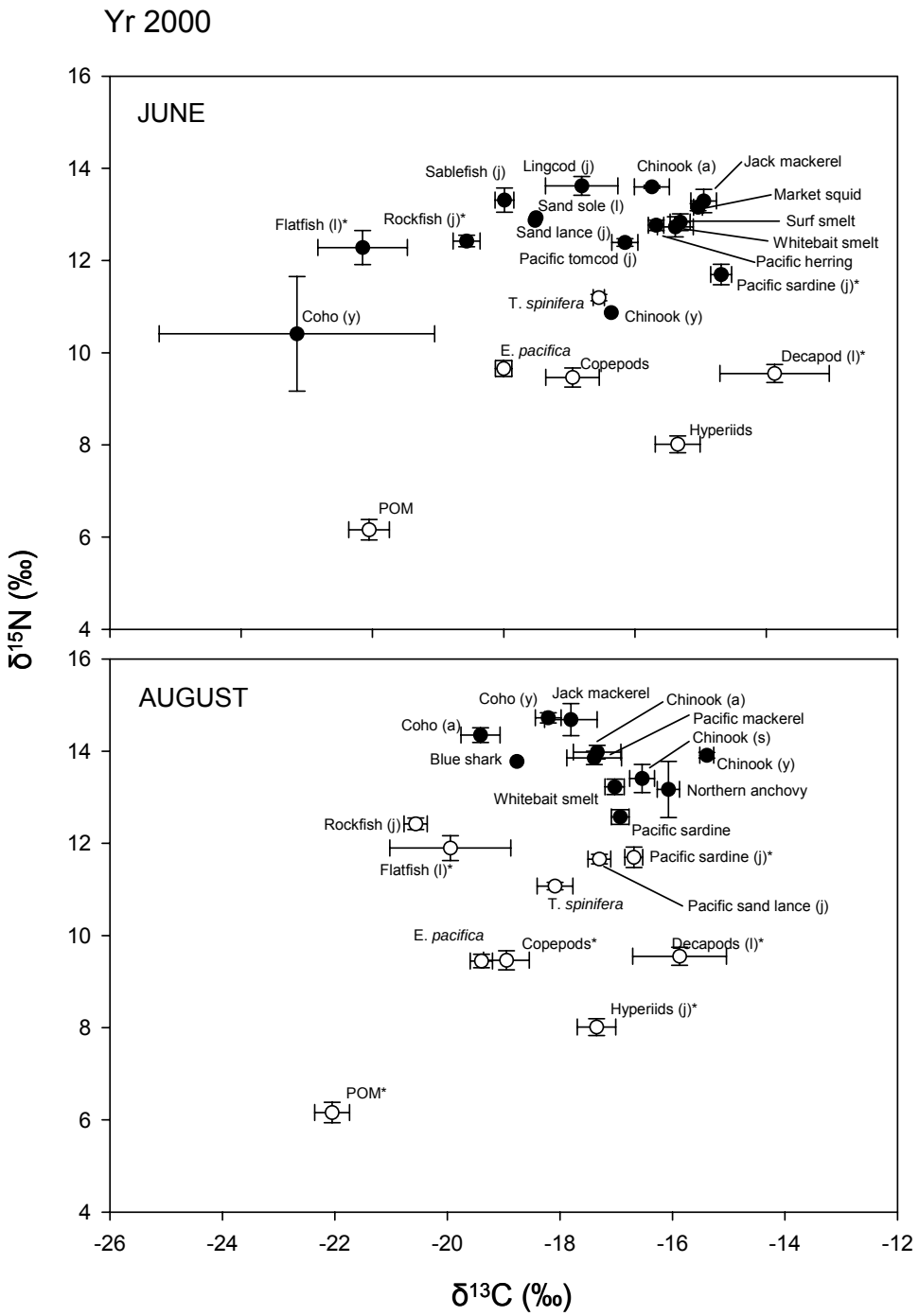

Figure 3.1. Mean and standard error of carbon and nitrogen stable isotope ratios of zooplankton (open circles) and nekton (closed circles) collected June (top) and August (bottom) 2000. Species labeled with an asterisk (*) were obtained from another cruise (see Table 1) to fill gaps in collection of trophically significant species.

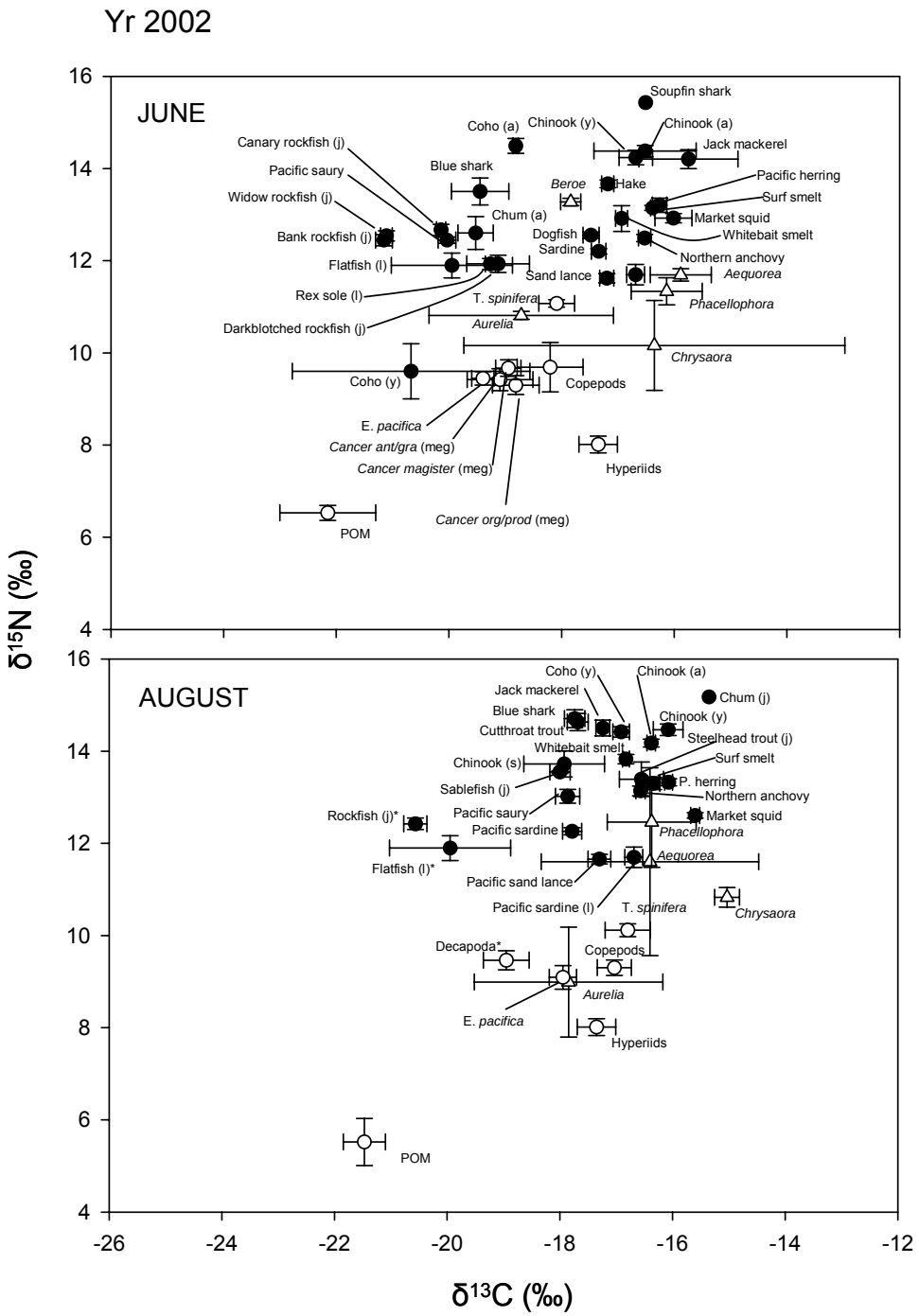

Figure 3.2. Mean and standard error of carbon and nitrogen stable isotope ratios of zooplankton (open circles) and nekton (closed circles) collected June (top) and August (bottom) 2002. Species labeled with an asterisk (*) were obtained from another cruise (see Table 1) to fill gaps in collection of trophically significant species.

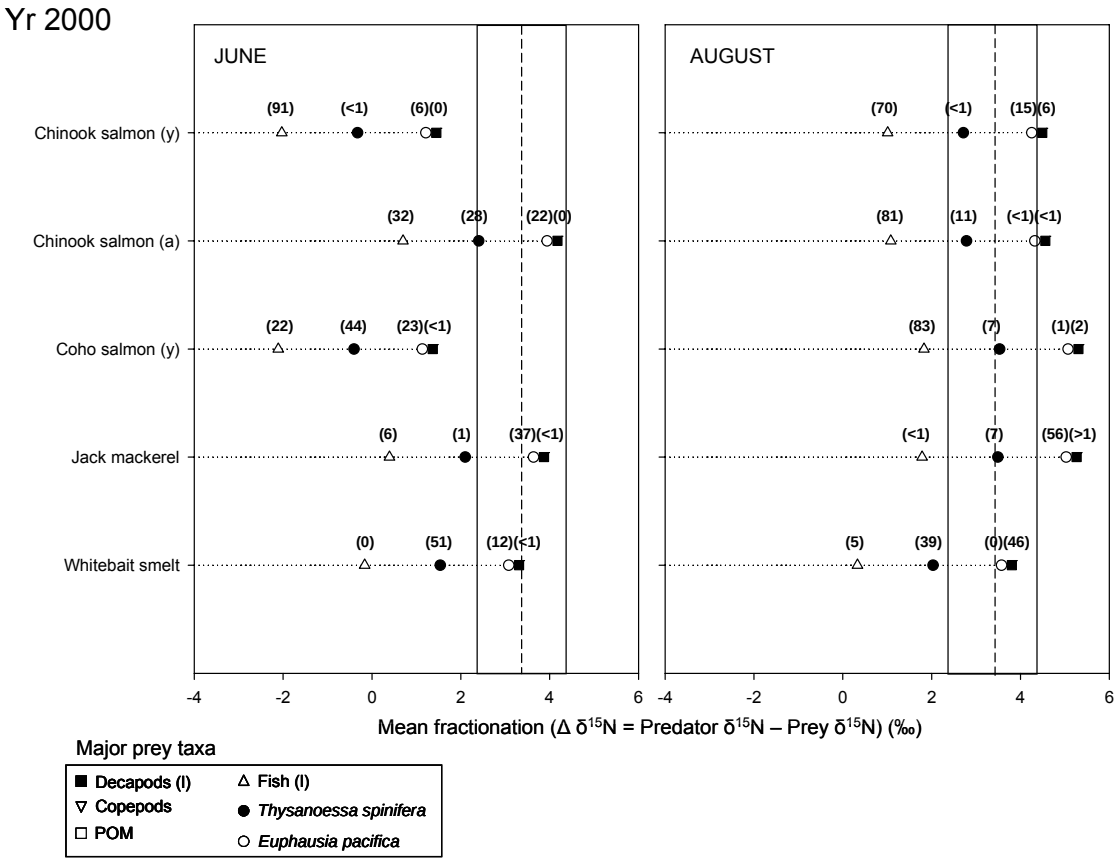

Figure 3.3. Mean δ15N fractionation (Δδ15N ‰) of consumers from major prey taxa during June and August of 2000. Dashed line and shaded region denote the expected mean and standard error trophic fractionation (3.4 ±1.8‰)(Post 2002), respectively. Numbers in parentheses above prey symbols are the percent wet weight contribution of prey to the predator's diet from stomach content analysis.

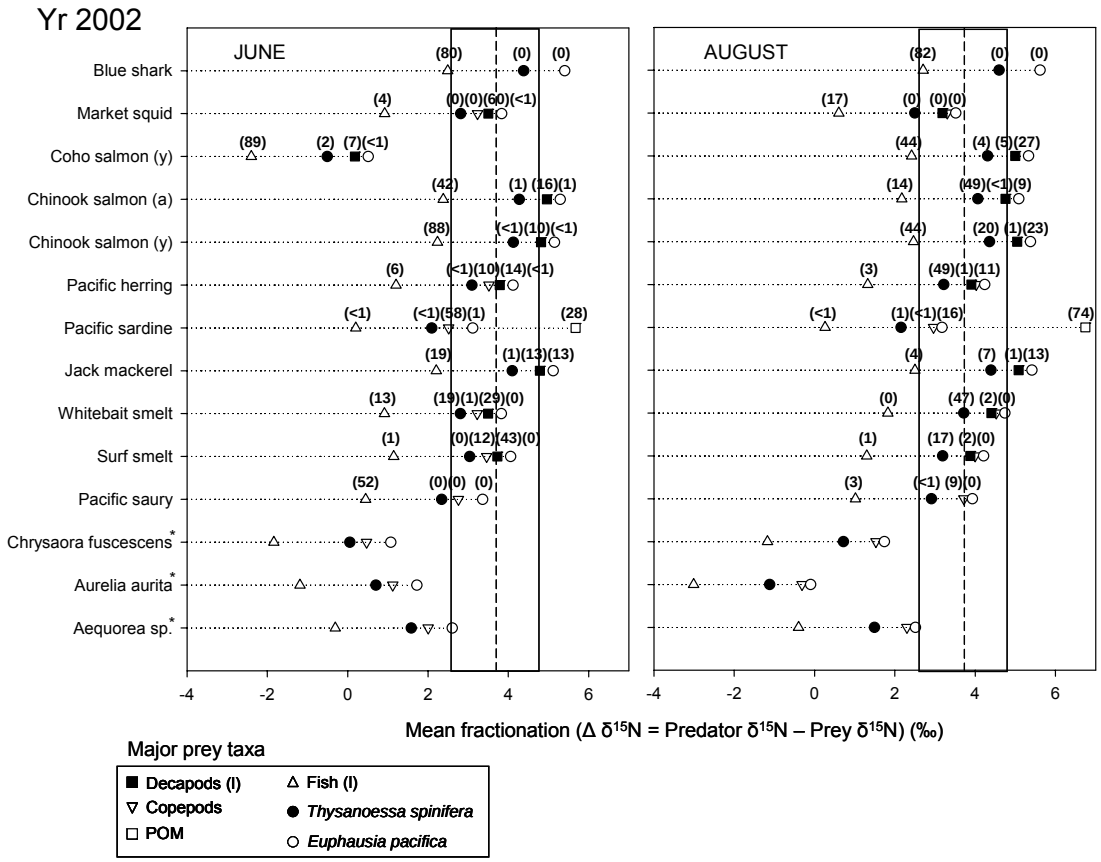

Figure 3.4. Mean δ15N fractionation (Δδ15N ‰) of consumers from major prey taxa during June and August of 2002. Dashed line and shaded region denote the expected mean and standard error trophic fractionation (3.4 ±1.8‰)(Post 2002), respectively. Numbers in parentheses above prey symbols are the percent wet weight contribution of prey to the predator's diet from stomach content analysis.

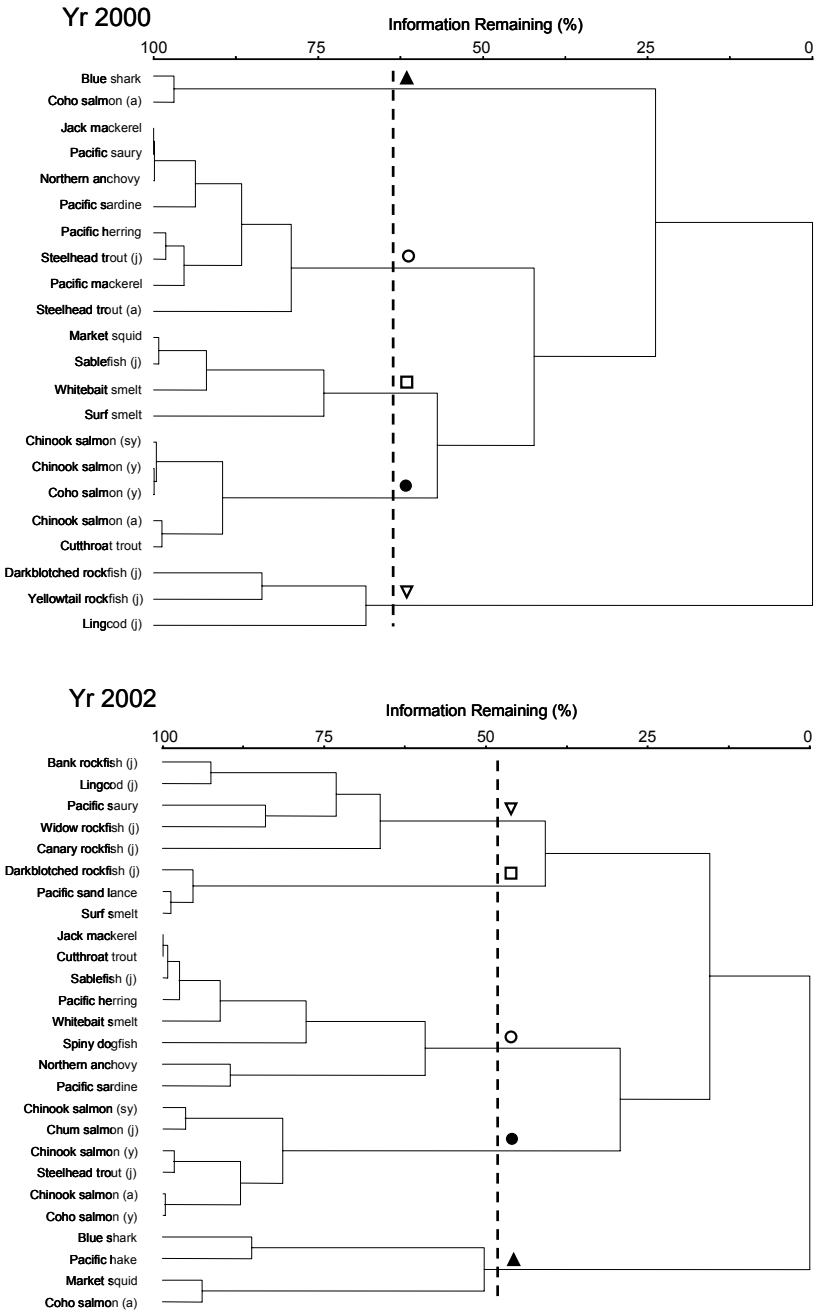

Figure 3.5. Cluster dendrograms from agglomerative hierarchichal cluster analysis (Relative Sorensen, Flexible beta) based on 2000 (top) and 2002 (bottom) contribution (percent wet weight) of major prey taxa to diet. Cutoff level is shown as the dotted line with major trophic groups defined as the following prey taxa: copepod/euphausiid furcilia/larval fish (upside-down open triangle); euphausiids/mixed prey of decapod larvae, larval fish, and hyperiid amphipods (open square); ichthyoplankton/euphausiids (closed circle); mixed Crustacea of larval decapods, amphipods and copepods/ichthyoplankton (open circle); adult fish/euphausiids (solid triangle).

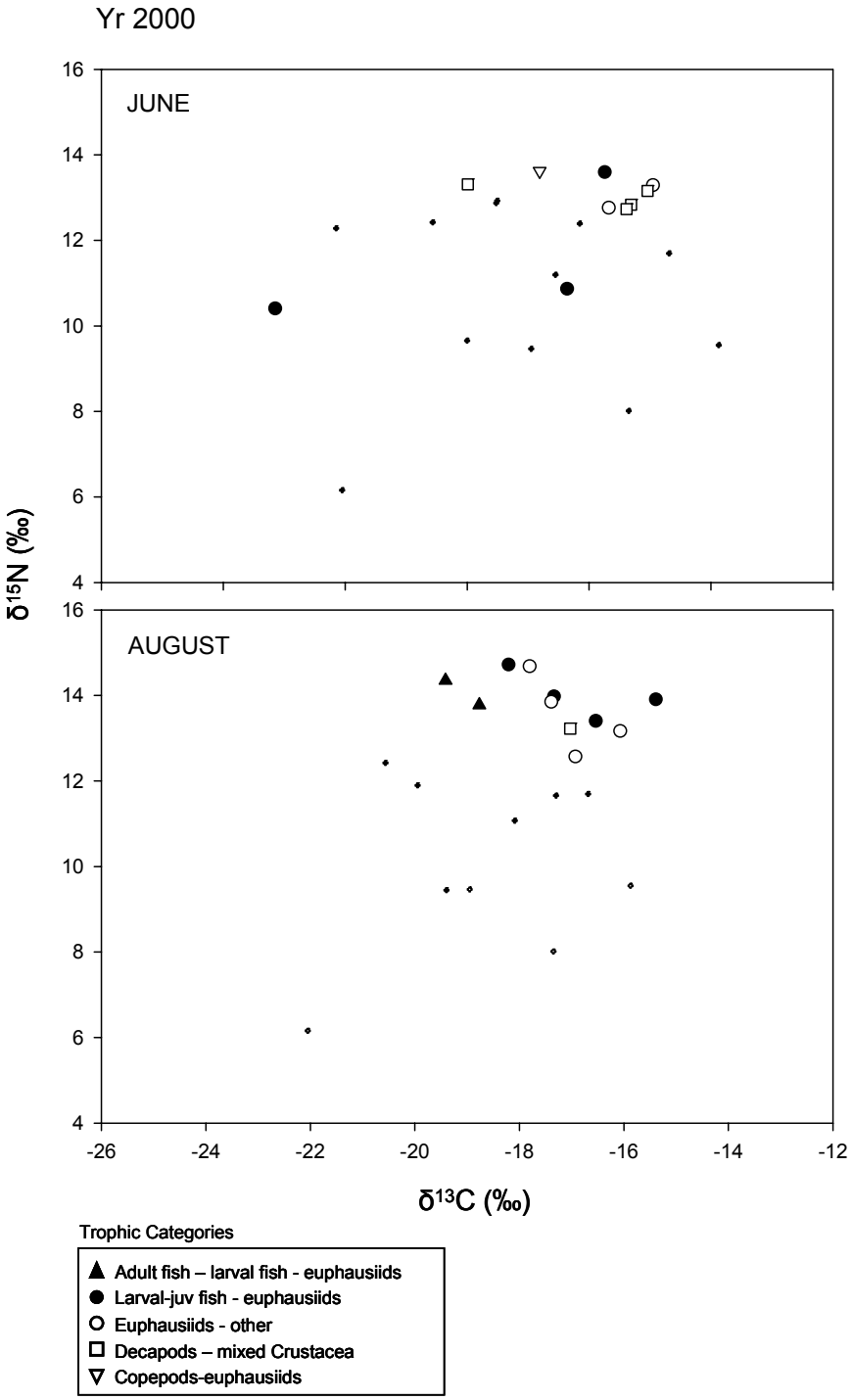

Figure 3.6. Mean carbon and nitrogen stable isotope ratios of nekton trophic groups based on agglomerative hierarchical cluster analysis of diet (percent wet weight) during June (top) and August (bottom) of 2000. Dots are species with no dietary information.

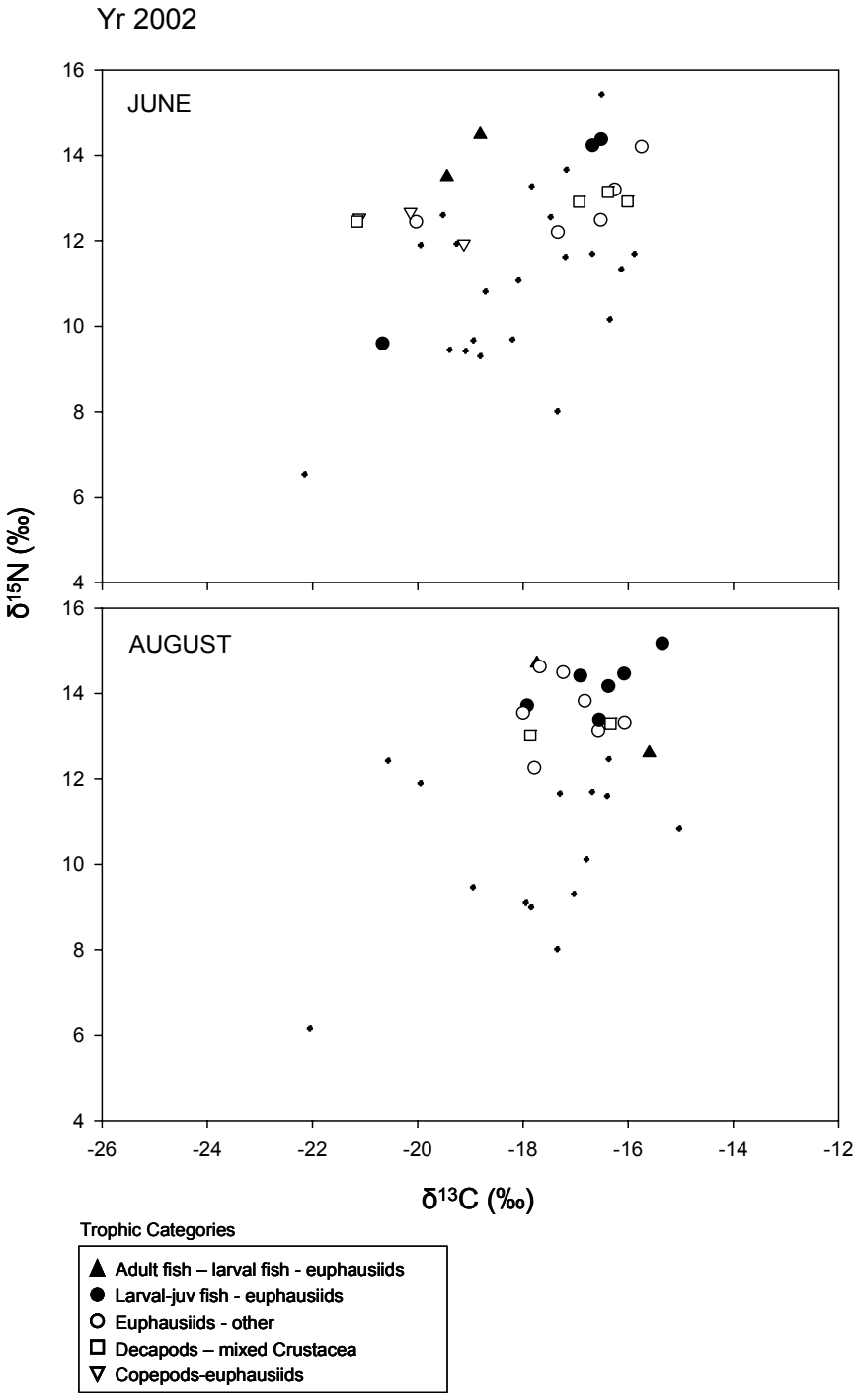

Figure 3.7. Mean carbon and nitrogen stable isotope ratios of nekton trophic groups based on agglomerative hierarchical cluster analysis of diet (percent wet weight) during June (top) and August (bottom) of 2000. Dots are species with no dietary information.

CHAPTER 4

CARBON STABLE ISOTOPES REVEAL RELATIVE CONTRIBUTION OF SHELF-SLOPE PRODUCTION TO THE NORTHERN CALIFORNIA CURRENT PELAGIC COMMUNITY

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ABSTRACT

Coastal upwelling regions exhibit strong cross-shelf hydrographic gradients or fronts that are associated with differences in primary production and community structure of higher trophic levels. This gradient is not wholly distinct, however, with cross-shelf movements of primary production and zooplankton occurring through advective currents and nekton through active migration. Carbon stable isotopes have been shown to be good tracers for linking benthic-pelagic coupling and nearshore and offshore production to higher trophic levels. To investigate the degree of nearhsore and offshore production utilized by multiple trophic levels across the Northern California Current (NCC) shelf-slope ecosystem, we examined the cross shelf distribution of $\delta^{13}C$ in nine species of nekton, three species of *Cancer* larvae, five gelatinous zooplankton, two dominant euphausiid species *Thysanoessa spinifera* and *Euphausia pacifica*, copepods (*Acartia* spp.) and particulate organic matter (POM). We compared the relationship of ^{13}C to sea surface temperature (SST), salinity (SSS) and chlorophyll-a. Results showed ^{13}C-enrichment from more nearshore (high SSS, low SST) sites relative to offshore (low SSS, high SST) sites at all trophic levels. Copepods and POM examined displayed a high degree of overlap, due in part to advection of nearshore production to offshore waters. Of the two dominant euphausiid species of the NCC system, the nearshore species, *T. spinifera,* was significantly more ^{13}C-enriched than the offshore species, *E. pacifica*. Gelatinous zooplankton expressed very high degrees of intraspecfic variation in $\delta^{13}C$ that were related to their onshore-offshore distributions. Nekton species associated with very nearshore waters had the highest $\delta^{13}C$ (-16.5‰) and offshore species of juvenile pelagic rockfish (-21.6‰), adult coho and chum salmon (-20.5 and 20.2‰, respectively) had the lowest, with many of the mid-shelf species having intermediate $\delta^{13}C$ values (-19.5 to -17.0‰). Because upwelling regions may contribute carbon to offshore oceanic gyres our study indicates $\delta^{13}C$ could be used as tracer of this contribution in linking large marine ecosystems.

INTRODUCTION

Continental shelf and slope pelagic ecosystems are typically associated with marked differences in primary production (Peláez and McGowan 1986, Thomas and Strub 2001) and community composition (Mackas 1984, Brodeur et al. 2005, Hunt and Hosie 2005), but are also connected through cross-shelf advective currents (Send et al. 1987, Morgan et al. 2003, Mackas and Coyle 2005), and active movement by larger organisms (Beamish et al. 2005). Delineating these systems and measuring their potential connectivity is problematic because of the dynamics of a fluid environment, organism mobility and constraints on sampling a large marine ecosystem. Cross-shelf advective processes of coastal upwelling have been the focus of recent investigations, in part because of the potential of hydrographic processes linking coastal to offshore basin ecosystems and the inherent links between changes in climate and atmospheric forcing (McFarlane and McKinnell 2005) and upwelling frequency and intensity. However, the extent to which shelf-slope ecosystems are connected at various trophic levels is not well understood.

The northern California Current (NCC) ecosystem resides approximately between central Vancouver Island (B.C. Canada) and Northern California. Between May and September the coastal shelf is characterized as having a nearshore band (water depth <150 m) of high production and an extensive area of relatively low production offshore (>150 m) (Lentz 1992). Differences between the two environments are also associated with species-specific assemblages of birds (Veit et al. 1996), fish (Brodeur and Pearcy 1992), and zooplankton (Cross 1964, Peterson et al. 1979). These systems therefore represent rather distinct habitats for transitory species that may overlap through hydrographic processes such as coastal upwelling and cross-shelf advection of primary and secondary production. Cross-shelf zonation of zooplankton and nekton has been described off the coast of Oregon and Washington (Cross 1964, Cross and Small 1967, Lough 1975, Pearcy 1976, Peterson et al. 1979, Brodeur and Pearcy 1992, Peterson and Keister 2002, Brodeur et al. 2005). Cross (1964) and Cross and Small (1967) described zonation of the

copepods *Acartia danae*, *A. longiremis*, *Pseudocalanus mimus* and *Centropages mcmurrichi*, and determined the latter three to be coastal species while *A. danae* was found primarily offshore. Peterson et al (1979) reported the copepod *Pseudocalanus* sp., *Acartia clausii*, and *Centropages abdominalis* to be most abundant in more nearshore waters, while *A. longiremis*, *Calanus marshallae* and *Oithona similis* appear to be more evenly distributed across the shelf. From sampling along two transects south and two north of Cape Blanco, Morgan et al. (2003) established three copepod species as being coastal (*P. mimus*, *A. longiremis*, and *C. marshallae*) and three (*Paracalanus parvus*, *Ctenocalanus vanus* and *Mesocalanus tenuicornis*) as offshore. Similar patterns have also been observed between larvae of *Cancer* spp. (primarily offshore) and more neritic-littoral species of shore and pea crabs (e.g. *Fabia subquadrata*, *Pinnixia littoralis*, and *Pachycheles*)(Lough 1975), euphausiid species (Gómez-Gutiérrez et al. 2005), and larval fish communities (Richardson and Pearcy 1977, Auth and Brodeur 2006).

The dynamics of offshore advection of zooplankton is not well understood, generally due to the complexity of the system and zooplankton behavior. Despite this, sustained levels of upwelling have been attributed to general patterns in offshore advection of certain zooplankton species (Pearcy 1976, Peterson et al. 1998). Zooplankton observed from high and low upwelling regions have shown predictable patterns with respect to nearshore and offshore copepod communities. For the NCC system, Peterson and Keister (2002) compared copepod community composition of offshore and nearshore sites from areas of known high (south of Cape Blanco) and low (north of Cape Blanco) upwelling, and found no difference between onshore-offshore communities in high upwelling areas, while lower upwelling areas were different. In a similar study, Morgan et al. (2003) observed offshore copepod communities to be significantly different between north and south of Cape Blanco, indicating that upwelling may have some influence on zooplankton community assemblages. These studies indicate the potential importance of upwelling in transporting biomass and shaping the zooplankton community structure of offshore waters; however little is known of the importance of nearshore production to higher trophic levels both from nearshore and offshore ecosystems.

The distribution of zooplankton species or taxonomic groups has proven to be an indicator of certain water masses (Cross and Small 1967, Peterson et al. 1998), but its application as a biological tracer is limited by an inability to differentiate between conspecifics or closely related species that may derived from different origins. Alternatively, the use of stable isotopes of carbon and nitrogen have been used as biological tracers to measure organism movement and migration patterns across ecosystems (Fry 1981, Peterson and Fry 1987, Hobson 1999). For carbon and nitrogen stable isotopes the potential use as a biological tracer movement requires a strong difference between the isotope signature of an organism's original food source relative to that of its new diet in a different environment (Fry and Sherr 1984). Carbon and nitrogen stable isotope ratios are heavier in marine compared to freshwater environments (Kline 1990), and this difference has been applied to examining migration in fish (Bilby et al. 1996), and the degree of marine and freshwater derived material within estuarine ecosystems (Fry 1999). However, some problems exist where the isotope signatures between environments are small and variation in trophic level enrichment of an organism exceeds this difference. For nitrogen, differences in $\delta^{15}N$ can occur at the level of primary production (Waser et al. 1998) and with increasing trophic level (approximately 3.4‰, Post 2002) and diet (e.g., amount of protein, McCutchan et al. 2003); for carbon, differences in $\delta^{13}C$ occur primarily at primary production with small increases with increasing trophic level (0.8‰ France and Peters 1997, Miller Chapter 3; 0.4‰, Post 2002). Therefore because $\delta^{13}C$ primarily fractionates at the primary production level and changes little with increasing trophic level, it often makes this a more effective tracer of organism movement across ecosystems with differing types of primary production. Within marine ecosystems $\delta^{13}C$ has been shown to differentiate benthic from pelagic-derived production (Haines and Montague 1979, Davenport and Bax 2002) and between nearhsore and offshore productivity (Perry et al. 1999), with nearshore and benthic systems being more enriched in $\delta^{13}C$. Stable isotope analysis of zooplankton from nearshore and offshore communities of the northeast Pacific have indicated a significant difference between the two environments. Perry et al. (1999) observed a ^{13}C-enrichment (relative to ^{12}C) from shelf and slope waters using particulate organic matter (POM),

zooplankton, and larval fish. Kline (1999) observed a similar ^{13}C-enrichment gradient in *Neocalanus cristatus* and "bulk zooplankton" between waters of Prince William Sound and the Gulf of Alaska.

In this study we investigated the use of $\delta^{13}C$ as a biological tracer of nearshore/shelf and offshore/slope primary production. If nearshore differences in primary production occur within this system, we hypothesized that this should be expressed as differences in $\delta^{13}C$, and that these should be transferred to higher trophic levels. To test this, we examined the distribution of $\delta^{13}C$ in organisms relative to cross-shelf differences in primary production and abiotic environmental factors indicative of shelf and slope waters.

METHODS

Collections of nekton and most zooplankton for this study occurred from Northeast Pacific Global Ocean Ecosystems Dynamics (GLOBEC) cruises during May/June (29 May – 18 June) and July/August (29 July – 18 August) 2000 and 2002. Sampling occurred along a series of transects across the shelf between Crescent City, California (Lat 41° 54.0') and Newport, Oregon (Lat. 44° 39.0') (Brodeur et al. 2004, Reese and Brodeur 2006). At each station various zooplankton and nekton species were collected using a Nordic-264 rope trawl (30 m wide by 18 m depth) and a surface neuston haul (1 m^2 mouth, 335 μm mesh; see Reese et al. 2005 for sampling details). Some zooplankton collections for decapod larvae and copepods were made from June and September 2002 cruises just to the north of our study region. Particulate organic matter (POM) samples were collected using a Niskin bottle sampled at 3 m depth. Niskin samples were pre-filtered through a 64 μm sieve to remove copepod eggs and zooplankton, then filtered through a 47 mm glass fiber filter (~0.7 μm) at <10 psi. All nekton, zooplankton and POM samples were immediately frozen (-20ºC) following collection at sea and later taken to the laboratory for processing. At each sampling location, sea surface temperature (SST, 3 m), salinity (SSS), and chlorophyll-*a* (chl-*a*) were measured. A detailed description of environmental data collection is provided in Reese and Brodeur (2006).

Laboratory

Laboratory processing of nekton and zooplankton involved identification, measurement and extraction of tissue for stable isotope analysis. Dorsal muscle tissue was extracted from nekton and larval/juvenile fishes, whereas whole body was used for zooplankton. A detailed description of this procedure, including preparation of samples for analysis is provided in Chapter 3 of this dissertation. For POM, samples were first acid treated to remove inorganic carbon. This was done by fumigating the POM filter with 12 molar HCL for 24 h. Samples were then dried in a drying oven for 24 h at 60° C. After drying, all samples were pulverized using a mortar and pestle, weighed and sent to one of two labs to measure stable isotope ratios. Most samples were analyzed at the National Marine Fisheries Service Northwest Fisheries Science Center (Seattle, Washington) isotope laboratory using a Costech ECS 4010 elemental analyzer coupled to a Thermo Electron Delta Plus stable isotope ratio mass spectrometer. Precision for the isotope analysis was $< \pm 0.3$ for $\delta^{15}N$ and $< \pm 0.2$ for $\delta^{13}C$. Nitrogen and carbon values were referenced to air and Vienna Pee Dee Belemnite, respectively. Remaining samples were analyzed at the National Aeronautics and Space Administration (NASA) Ames Research Center (Moffett Field, California) using a Carlo Erba 1108 elemental analyzer coupled to a Finnigan Mat, Delta Plus mass spectrometer; instrument precision for carbon and nitrogen were ±0.08 and ±0.25, respectively. Stable isotopes are measured as the ratio of the heavy (^{13}C and ^{15}N) to the lighter (^{12}C and ^{14}N) isotope of an element using the following equation: $\delta X = [(R_{sample}/R_{standard})] \text{ X } 10^3$, where X is ^{13}C or ^{15}N and R is the ratio of the heavy to light isotope (Peterson and Fry 1987). After analyses, carbon isotope were lipid-adjusted using an equation devised by McConnaughy and McRoy (1979) and Wada et al. (1987). This was performed because lipids can influence carbon isotope ratios by retaining the lighter carbon isotope (C^{12}) over the heavier (C^{13}) (McConnaughy and McRoy 1979). Stable carbon isotopes can also be influenced by trophic-level enrichment (Rau et al. 1983), with an average of 0.4‰ (Post 2002) to 0.8‰ (France and

Peters 1997) increase per trophic level. To correct for this we applied the following equation by Kline (1997) to normalize for trophic level differences:

$$\delta^{13}C'_{TL} = \delta^{13}C' - \epsilon_c/\epsilon_n \, (\delta^{15}N_{sample} - \delta^{15}N_{reference}) \qquad (1)$$

where, $\delta^{13}C'_{TL}$ is the trophic level normalized $\delta^{13}C$ based on the $\delta^{15}N$ of the sample relative to a reference $\delta^{15}N$, ϵ_c and ϵ_n represent the trophic fractionation of carbon and nitrogen, respectively. For our study we used the overall average copepod $\delta^{15}N$ (10.01‰) as the reference trophic level, and fractionation factors (ϵ) of 1.0 for ϵ_c and 3.4 for ϵ_n as the amount of $\delta^{13}C$ and $\delta^{15}N$ enrichment per trophic level (Kline 1997). Copepods were used as the reference level because as grazers they provide the most consistent link between POM and higher trophic levels.

Data Analyses

Several methods were used to compare nearhsore-offshore differences in ^{13}C and to relate any differences observed to biotic and abiotic factors. For POM and copepods, nearshore (i.e. shelf) and offshore (i.e. slope to oceanic) samples were delineated as those collected in waters with bottom depths of <150 m and >150 m, respectively, following Lentz's (1992) delineation of shelf and slope waters. Comparisons between nearshore and offshore collections were performed separately for the two sampling periods using a Student's t-test for differences in the means ($\alpha = 0.05$; Zar 1998). For differences between multiple species, we applied ANOVA ($\alpha = 0.05$) and Tukey Honestly Significant Difference (HSD) test. Multiple linear regression methods (backwards, stepwise) were used to examine the relationship between $\delta^{13}C$ and the parameters SST and SSS; for POM samples we additionally examined the relationship of log·chl-*a* (ug/L) to $\delta^{13}C$. The full model containing all parameters was reduced by removing parameters not statistically significant (i.e. $p>0.05$) to form the final reduced model.

RESULTS

POM

From June and August 2002 cruises particulate organic matter (POM) showed a significant difference in $\delta^{13}C$ between nearshore and offshore sites (t-test, $p<0.0001$, Fig. 4.1) with nearshore enriched relative to offshore on average 3.11 and 1.69‰ for June and August, respectively (Table 4.1). Stepwise backwards multiple linear regression analyses of parameters sea surface temperature (SST), salinity, and log (chl-*a*) resulted in significant correlations of log (chl-*a*) for June and log (chl-*a*) and salinity for August. For June the model $\delta^{13}C = 23.5194 + 1.42924 \times \log(\text{chl-}a)$ explained 68% of the variation observed; the August model $\delta^{13}C = 41.6823 - 1.91909*SSS + 0.941562 \times \log(\text{chl-}a)$ explained 46% of the variation (Fig. 4.2). When salinity was removed from the August model, log (chl-*a*) was able to explain 23% of the variation. For both months combined, the minimum and maximum $\delta^{13}C$ values associated with corresponding minimum and maximum chl-a were -25.05 and -18.67, respectively. Chlorophyll-*a* was only significantly correlated with SST during June ($p>>0.001$, $r^2 = 0.62$), but was not correlated with SST or SSS in August ($p<0.1$).

Zooplankton

Comparison between copepods collected nearshore and offshore for both cruises showed a general trend of higher $\delta^{13}C$ from nearshore relative to offshore (students t-test, $p = 0.06$, Fig. 4.3) and small samples precluded robust statistical testing of August samples (Table 4.1). For June, multiple linear regression showed SST and SSS were both non-significant ($p>0.10$). The euphausiid species *Euphausia pacifica* and *Thysanoessa spinifera* were only collected together during the August cruise. *Thysanoessa spinifera* was significantly more enriched in ^{13}C (Students t-test $p=0.01$, mean difference in $\delta^{13}C = 1.09$‰). Multiple linear regressions of SST and SSS were non-significant for both species (model $p>0.10$). Analysis of three species of *Cancer* spp. megalopae, *C. magister*, *C. antennarius*/*gracilis*, and *C. oregonensis*/*productus* showed no significant differences in $\delta^{13}C$ among the three species (ANOVA, Tukey HSD test, $p>0.05$).

Table 4.1. Summary of sample size (N), and δ13C mean and standard error (SE) of each species/taxonomic group collected during June and August 2002 cruises. Species are adult stages unless noted in parentheses as megalopa larvae (l), juvenile (j), yearling (y) or adult (a).

	June			August		
Taxa	**N**	**Mean $\delta^{13}C$**	**SE**	**N**	**Mean $\delta^{13}C$**	**SE**
POM						
Slope	15	-23.69	0.30	24	-22.13	0.40
Shelf	15	-20.58	0.37	14	-20.44	0.38
Zooplankton						
Copepoda (slope)	17	-18.18	0.41	2	-17.09	0.64
Copepoda (shelf)	9	-16.69	0.26	17	-16.42	0.31
Thysanoessa spinifera				5	-16.57	0.42
Euphausia pacifica				5	-17.66	0.30
Cancer oregonensis/productus (l)	20	-18.64	0.27			
Cancer magister (l)	14	-18.47	0.44			
Cancer antennarius/gracilis (l)	11	-18.22	0.65			
Gelatinous Zooplankton						
Aequorea victoria	19	-16.20	0.53	14	-17.24	0.32
Phacellophora camtschatica	9	-16.82	0.64	2	-16.87	0.55
Aurelia aurita	4	-17.57	1.62	11	-15.35	0.54
Chrysaora fuscescens	17	-15.16	0.12	6	-14.77	0.27
Beroe	9	-18.54	0.19			
Nekton						
Market squid	9	-16.63	0.12	6	-16.10	0.10
Spiny dogfish	9	-18.01	0.12			
Coho salmon (a)	8	-20.21	0.13			
Chum salmon (a)	2	-20.06	0.31			
Chinook salmon (y)	3	-17.53	0.23	27	-17.08	0.26
Chinook salmon (a)	17	-17.50	0.21	30	-17.31	0.08
Cutthroat trout				8	-18.73	0.19
Steelhead trout (j)				4	-17.29	0.47
Pacific sand lance (j)	22	-17.47	0.20			
Surf smelt	2	-17.09	0.05	4	-17.12	0.13
Whitebait smelt	12	-17.51	0.07			
Northern anchovy				1	-17.08	
Pacific sardine	10	-17.79	0.14	15	-18.19	0.19
Pacific herring	15	-16.95	0.13	24	-16.77	0.07
Jack mackerel	1	-16.35		7	-18.20	0.14
Rockfish (pelagic, j)	24	-21.17	0.21			
Pacific saury				11	-18.51	0.23

Multiple linear regression of $\delta^{13}C$ as a function of SST and SSS for the three species resulted in a reduced model for *C. magister* with only with SSS as a significant variable ($p<0.0001$); the reduced model $\delta^{13}C = -10.3 – 0.38 \times SSS$ was able to explain 50% of the variation. Comparison of gelatinous zooplankton from June showed that *Beroe* was significantly depleted in ^{13}C compared to *C. fuscescens*, *Aurelia aurita*, *Aequorea victoria* and *P. camtschatica* (Fisher's LSD test, $p=0.0002$, mean difference in $\delta^{13}C$ of 3.38, 2.5, 2.34, and 1.72‰, respectively), and *C. fuscescens* was significantly different from *P. camtschatica* (mean difference = 1.66‰). Multiple linear regression of $\delta^{13}C$ of all species combined as a function of SST and SSS resulted in SST being the only significant parameter ($p<0.01$), in the following reduced model: $\delta^{13}C = - 12.39 – 0.37 \times SST$ ($r^2 = 0.18$); a plot of this model by individual species shows species-specific tends in $\delta^{13}C$ and temperature (Fig. 4.4). During August *Chrysaora fuscescens* had the highest $\delta^{13}C$, followed by *Aequorea victoria*, *Phacellophora camtschatica, Aurelia aurita* and *Beroe* (Table 4.1). *Aequorea victoria* was significantly depleted in ^{13}C from *C. fuscescens* (mean difference = 2.46‰) and *Aurelia aurita* (mean difference = 1.89‰). Multiple linear regression of combined species resulted in temperature as the significant parameter in the following model: $\delta^{13}C = -9.42 – 0.67*SST$ ($p<<0.001$, $r^2 = 0.55$). A plot of this model by individual species shows species-specific trends in $\delta^{13}C$ and SST (Fig. 4.4); *C. fuscescens* was most restricted to cooler temperatures and displayed the most enriched $\delta^{13}C$ values whereas *P. camtschatica*, *Aurelia aurita*, and *Aequorea victoria* were more widely-dispersed across temperatures but displayed general within-species trends of increasing $\delta^{13}C$ with lower temperatures.

Nekton

Comparisons of nekton species were limited to entirely marine species and adult stages of salmonids that had resided in the ocean environment for >1yr; therefore, yearling-juvenile coho salmon, chinook salmon and chum were excluded from the analysis. During June juvenile rockfish species (darkblotched - *Sebastes crameri*, widow - *S. entomelas*, canary - *S. pinniger*, and bank - *S. rufus*) were the most ^{13}C-depleted (mean $\delta^{13}C = -21.17$‰), followed by adult coho and chum salmon (mean = -20.21 and -

20.06‰, respectively), spiny dogfish and Pacific sardine (mean = -18.01 and -17.9, respectively)(Table 4.1). Species more enriched in ^{13}C were surf and whitebait smelt, adult Chinook salmon, Pacific herring, sardine, jack mackerel and market squid (group mean = -17.2 ± 0.09‰). Multiple linear regression of species combined $\delta^{13}C$ with SST and SSS resulted in SSS being the only significant parameter ($p<0.01$) in the following model: $\delta^{13}C = -43.74 + 0.79*SSS$ ($r^2 = 0.15$, Fig. 4.5). From this model, juvenile rockfish species were primarily associated with lower $\delta^{13}C$ (mean = -21.17 ± 0.21‰) and lower salinities (mean = 31.6 psu, Fig. 4.5), with more ^{13}C-enriched species of Pacific herring, smelt species, market squid and adult Chinook salmon associated with higher salinities (mean = 32.9 psu); Pacific sand lance appeared in more mid-SSS (mean = 31.5 psu) and displayed $\delta^{13}C$ values similar to species collected at slightly higher SSS's (mean = -17.3‰). Adult coho and chum salmon displayed the lowest $\delta^{13}C$ values but were largely dispersed across the entire SSS gradient measured (group range = 30.2 – 33.9 psu). When adult coho and chum salmon were removed from the June regression model, SSS remained significant however the r^2 value was only moderately improved ($p=0.01$, $r^2 = 0.18$).

During August, nekton most ^{13}C-depleted were cutthroat trout, Pacific saury, jack mackerel, and Pacific sardine (group mean = -18.4 ± 0.13‰), with more enrich species being adult Chinook salmon, northern anchovy, surf smelt, Pacific herring and market squid (group mean = -16.9 ± 0.16‰). Multiple linear regression of $\delta^{13}C$ as a function of SST and SSS resulted in SSS as the only significant parameter ($p>0.001$) for the following reduced model $\delta^{13}C = -60.4471 + 1.29122*SSS$ ($p<0.0001$, $r^2 = 0.42$, Fig. 4.6). Pacific herring, yearling Chinook salmon, surf smelt, northern anchovy and market squid were more enriched in ^{13}C (group mean = 33.5 psu) and were associated more with higher salinities (group mean = 33.5 ± 0.04 psu); Jack mackerel and Pacific saury resided in the lowest salinities (mean = 32.2 and 32.7 psu, respectively) and had the lowest $\delta^{13}C$ values (mean = -18.2 and -18.5‰, respectively).

DISCUSSION

Our study revealed a general shelf-slope trend in decreasing $\delta^{13}C$ within multiple trophic levels of the pelagic community, providing a relative measure of a species shelf and slope-oriented base production in the food web. Differences in $\delta^{13}C$ of multiple trophic groups were either associated with cross-shelf changes in SST and/or SSS. Based on differences in chl-*a* distribution it appears that $\delta^{13}C$ fractionation at the base of the food web was due to the spatial differences in diatoms in nearshore and shelf waters compared to smaller phytoplankton in offshore-slope waters. The trend in zooplankton varied by taxonomic group; copepods displayed a measurable difference between shelf and slope waters, however there was a high degree of variation and overlap between the two groups which may have been due to advection of nearshore species to slope waters. Euphausiids *T. spinifera* and *E. pacifica* were different in $\delta^{13}C$, with the shelf species, *T. spinifera*, being more ^{13}C-enriched relative to the slope species, *E. pacifica*. *Cancer* spp. larvae generally displayed a more offshore-slope signature, which is in general agreement with the offshore distribution of early larval stages in this taxonomic group (Reilly 1983). One exception was a linear increase in $\delta^{13}C$ with SSS in *C. magister*, indicating this species may be more widely dispersed across the shelf and slope. Nekton species displayed variable $\delta^{13}C$ values with several species that are highly ^{13}C-enriched or depleted being associated with nearshore or offshore waters, respectively. Many of the species collected on the shelf expressed $\delta^{13}C$ signatures intermediate between the nearshore and offshore taxa, suggesting that these species are obtaining food from both adjacent nearshore and offshore systems.

Our results show a delineation of the NCC pelagic food web that can serve as a basis for modeling subcomponents of the NCC ecosystem. Likewise, the use of $\delta^{13}C$ to measure organism movement by advective currents could be applied to linking the NCC system to the Pacific Ocean basin ecosystem. This effort should apply cross-ecosystem sampling at multiple trophic levels and depths to observe surface and subsurface advection of zooplankton and primary production. The following analysis of subsystems serves as our argument.

POM

The cross-shelf distribution of $\delta^{13}C$ in multiple trophic levels provided a relative measure of cross-shelf dependence on nearshore versus offshore primary production. From POM samples, we observed greater fractionation in offshore samples, resulting in significant differences between the two sampling regions. This difference may be due, in part, to the predominance of diatoms in more nearshore waters. Within the same area and time of our study, Sherr et al. (2005) observed a higher fraction of diatoms nearshore of the upwelling front associated with chl-a measures >5µg/l, with smaller phytoplankton (<5µm coccooid cyanobacteria and eukaryotic phytoplankton) being more abundant in samples offshore of the front. Our analysis of chl-a and $\delta^{13}C$ showed a logarithmic relationship of increasing $\delta^{13}C$ and log chl-a (Fig. 4.2); values >5.0 µg/l were typically associated with less-fractionated $\delta^{13}C$ values of ~20.33‰ whereas values <3.0 µg/l had a mean of -22.8‰. The mechanisms behind this difference in carbon fractionation (ϵp) from phytoplankton are not clearly understood and are likely due to a complex of various factors (Rau et al. 1993). Growth rate (μ) and $[CO_2]_{aq}$ have been the primary factors attributed to differences in ϵp (e.g., Laws et al. 1995, Rau et al. 1997, Hofmann et al. 2000, Gervais and Riebesell 2001), but day length and irradiance (Thompson and Calvert 1994), nitrate limitation (Burkhardt et al. 1999) and other factors may interact and further influence ϵp. Tortell et al. (2000) determined diatoms were able to store $[CO_2]_{aq}$ through what is termed a carbon concentrating mechanism (CCM) which allowed for μ independent of extracellular $[CO_2]_{aq}$, thus decoupling differences in ϵp due to $[CO_2]_{aq}$; this was also suggested by Woodworth et al. (2004). Tortell et al. (2000) further speculated that low ϵp in their study was probably attributed to low carbon leakage from the cell and active (direct) uptake of HCO_3^-.

The range of $\delta^{13}C$ in our POM samples were within the range observed in marine phytoplankton from other studies (-23 – -18.5‰ at 45ºN latitude, Hofmann et al. 2000, and -23 – -21‰ off Oregon, Bosley et al. 2004). Lower (more negative) $\delta^{13}C$ values from this range however, appear too fractionated to account for the $\delta^{13}C$ values observed in higher trophic levels. After correcting for trophic level ^{13}C-enrichment, most

zooplankton and nekton remained ~2-3‰ enriched relative to POM (Fig. 4.7). Several reasons for this may be: *i*) the fractionation correction factor (eqn. 1) underestimated trophic fractionation in $\delta^{13}C$; *ii*) we failed to obtain the most enriched nearshore signatures of base production; *iii*) POM samples were not representative of selective utilization of base production by primary consumers, and/or *iv*) a more benthic source of food is being utilized.

The fractionation correction factor (eqn. 1) most likely did not account for much of the difference because after initial corrections, most species remained as much as 3‰ from base production, well beyond the generally-accepted 0.8‰ (France and Peters 1997, Miller Ch3 Dissertation) to 0.4‰ (Post 2002) enrichment per trophic level. Our POM samples may have missed the true nearshore signature of primary production. However, based on chl-a versus $\delta^{13}C$ of POM samples, increased diatoms in our samples failed to enrich samples beyond approximately -18.7‰, indicating that we probably obtained the full range of $\delta^{13}C$ from POM samples (Fig. 4.2). POM samples may not have been a true representation of the specific phytoplankton groups being utilized by primary consumers and carbon available to higher trophic levels. In our study, nearshore POM samples probably contained a high fraction of diatoms although the sample would have also been diluted by some proportion of non-photosynthetic material (del Giorgio and France 1996). Finally, the enrichment of certain species may be due to utilization of more benthic-oriented prey that typically have higher $\delta^{13}C$ values (Haines and Montague 1979, Fry and Sherr 1984, Hobson et al. 1995). Market squid, Pacific herring, northern anchovy and surf smelt, and most of the gelatinous zooplankton (excluding *Beroe*) had $\delta^{13}C$ values well above what would be predicted based on $\delta^{13}C$ of nearhsore POM. However, it is unlikely their signatures were derived from a benthic source because these species (mainly Pacific herring, northern anchovy and surf smelt) are obligate zooplanktivores (Miller, Chapter 2 this Dissertation) feeding on zooplankton which consume more surface-oriented primary and secondary production. It is more likely the discrepancies between POM and higher trophic levels is due to the selective feeding of phytoplankton by copepods and other primary consumers and that our POM samples obtained the

signature from utilized and non-utilized material. Future work should focus on better separation of POM samples into species-specific $\delta^{13}C$ values to determine base production most utilized by the higher trophic levels.

A significant hydrographic feature within our study region comes from freshwater influence from the Columbia River Plume (Barnes et al. 1972, Hickey and Banas 2003). During spring and summer months the Columbia River forms a distinct freshwater plume which extends across the shelf and move southward with the prevailing California Current (Barnes et al. 1972). One might reasonably conclude that more fractionated freshwater-based production would influence the $\delta^{13}C$ of offshore POM and possibly higher trophic levels. Several lines of evidence indicate this did not occur. The $\delta^{13}C$ trend has been observed in other regions where there is little offshore freshwater influence, including Vancouver Island, British Columbia (Perry et al. 1999) and northern California (Sydeman et al. 1997). From the Bering, Sea Guo et al. (2004) observed no freshwater influence of POM $\delta^{13}C$ in close proximity to a large river (Yukon River). This suggests that, at least in the systems mentioned above, that the dynamics of $\delta^{13}C$ shift in primary production from freshwater to marine environments is relative rapid.

Zooplankton

Copepods from shelf and slope samples were marginally non-significantly ($p = 0.06$) different in $\delta^{13}C$ between nearshore and offshore sites, and showed no significant correlation with $\delta^{13}C$ and shelf-slope parameters SSS or SST. Although differences were non-significant, there was a consistent trend of more ^{13}C-enriched copepods nearshore relative to offshore (Fig. 4.3). A problem was our limited sample size of slope copepods collected during spring which did not provide an adequate number for statistical comparison (this was due to machine error and I am in the process of resubmitting samples to increase the sample size). However, during this time upwelling strength and persistence was generally high within the system (Fig. 4.8) and the apparent lack of difference between nearshore and offshore copepods may have been due to offshore advection. The copepods measured for this study were primarily *Acartia* spp, which are

small (prosome length ~ 0.7-1.0 mm) and more prone to advective currents (Wroblewski 1980, Morgan et al. 2003). The dynamics of zooplankton distribution and coastal advection are complex because of sporadic versus persistent upwelling, and temporal changes in copepod life history stage, behavior (vertical migration) and age-specific mortality (Wroblewski 1980, 1982). Using simulations of the nearshore copepod *Acartia clausii* distribution during constant and intermittent upwelling, Wroblewski (1980) determined upwelling over a 3 d period enhanced advection, and after persistent upwelling during a 10 d period *A. clausii* could be found as far as 25 km offshore. Carbon isotope turnover in copepods has not been examined however some evidence suggests that isotope turnover in copepods from our study likely exceeded the duration of time for advection in this system. On the Bering Sea shelf, Schell et al. (1998) observed $\delta^{13}C$ values in copepods and euphausiids that coincided with advective currents from the central Bering Sea through the Bering Strait, a distance well beyond the shelf slope interface of the NCC. For the NCC system, continued work along the shelf-slope waters along the coastal upwelling gradient should be undertaken to determine the influence of upwelling and coastal advection on primary consumers.

Stable isotope studies of aquatic systems often use copepods over POM samples as a reference for the food web (Vander Zanden and Rasmussen 2001), in part because they represent the true signature of base production utilized and are less prone to short-term (e.g., days) fluctuations in primary production. The $\delta^{13}C$ of copepods in our study provided a reasonable correspondence of shelf and slope copepods to higher trophic levels (Fig. 4.7). For shelf copepods the bottom interquartile value of -15.8‰ (Fig. 4.7, line B) corresponds well to the most enriched nekton, gelatinous zooplankton and the dominant euphausiid on the shelf, *Thysanoessa spinifera* (Gómez-Gutiérrez et al. 2005). Slope copepods, however, displayed extreme interquartile ranges between -16.5 and -19.8‰, suggesting that the higher end (i.e. more enriched) values may have some fraction of copepods from nearshore waters, and that the lowest $\delta^{13}C$ of -19.8 (Fig. 4.7, line A) may be of copepods from a slope-offshore origin. The mean and lower interquarile range of slope copepods corresponded well to most mid-shelf and slope

species of nekton, the ctenophore *Beroe* sp., *Cancer* spp. megalopae, and the more slope-oceanic species of euphausiid, *Euphausia pacifica* (Gómez-Gutiérrez et al. 2005). The more oceanic species of adult chum and coho salmon (Beamish et al. 2005) and juvenile rockfish species (Brodeur et al. 2004) were predominantly well below the range of copepods collected from slope waters.

Many of the gelatinous zooplankton displayed some degree of intraspecific increases in $\delta^{13}C$ with decreasing temperature, which is consistent with the pattern of cooler upwelled water being associated with nearhsore shelf production (Thomas and Strub 2001). Gelatinous zooplankton characteristically exhibit high rates of consumption (Suchman et al. submitted) and growth (Larson 1986) which would result in rapid uptake of the localized $\delta^{13}C$ in zooplankton. Most of the *Cancer* spp. larvae displayed lower $\delta^{13}C$ values more indicative of offshore production. Of the *Cancer* spp. examined, *Cancer magister* exhibited a significant relationship of increasing $\delta^{13}C$ with increasing SSS, with higher SSS corresponding to more nearshore upwelled water (Huyer 1977). Growth rates in *C. magister* larvae are very high (Sulkin et al. 1996) and individuals may also rapidly assimilate the localized isotope signature of their prey, and/or the species may be widely dispersed across the shelf and individuals may be retained in specific water masses associated with nearshore or offshore production. Curtis et al. (2003) observed *C. magister* megalopae recruited to estuaries from a variable range of water types, indicating this species may be widely distributed across different water masses. The apparent lack of this trend in the two other *Cancer* spp. may be due to species-specific differences in growth and distribution or possibly the limited sample size in these species across SST and SSS gradients.

Nekton

Trends in higher $\delta^{13}C$ of shelf-slope oriented nekton were evident in the relationship with SSS (Fig. 4.5 and 4.6), with higher SSS associated with more nearshore upwelled water (Huyer 1977). Within this relationship, more nearhshore, high SSS and $\delta^{13}C$ species were market squid, Pacific herring and northern anchovy, whereas more offshore, low SSS and

$\delta^{13}C$ fishes were pelagic juvenile rockfishes and Pacific saury; most other nekton $\delta^{13}C$ values resided between the nearhsore and offshore-specific species (Fig. 4.5 and 4.6). This distribution is similar to that described by Bordeur and Pearcy (1992) in which the shelf-slope ecosystem can be divided into a near, mid and offshore pattern. Adult Coho salmon and to a lesser extent adult chum salmon added considerable variability in the general trend (Fig. 4.5). Both adult stages of these species maintain an oceanic existence (Beamish et al. 2005) and are likely in the coastal-shelf during this time preparing for freshwater migration to spawn. Species with more intermediate $\delta^{13}C$ values, such as jack mackerel, spiny dogfish and Pacific sardine, are highly mobile and may feed on adjacent nearshore and/or offshore production, either through active swimming or passive drift of prey by upwelling and downwelling.

Other studies have examined nearshore-offshore differences of $\delta^{13}C$ in nekton but not to the extent of trophic levels observed here. Sydeman et al. (1997) observed that more slope-oriented species of small fishes (including zooplankton and birds) had more negative $\delta^{13}C$ values, and deduced that nearhsore-offshore differences in $\delta^{13}C$ existed off northern California. Davenport and Bax (2002) observed no significant difference in fish across the southeast Australian shelf and attributed differences in $\delta^{13}C$ between benthic and pelagic production. Sherwood and Rose (2005) also observed very little difference between nearhsore and offshore-collected fish from the Newfoundland-Labrador shelf food web. The relative distinction between nearshore and offshore species at higher trophic levels within the NCC system is probably due to the more structured shelf and slope waters from upwelling (Lentz 1992) and our focus on more pelagic species. Other systems such as the Georges Bank (Fry 1988, Wainright and Fry 1994) and Scotian Shelf (Mills et al. 1984) have displayed little or no apparent $\delta^{13}C$ differentiation between nearshore and more offshore species. This may be due in-part to their relatively shallow, well-mixed waters allowing for more benthic-pelagic coupling to occur, and the absence of strong coastal upwelling that form fronts and thus structure to pelagic ecosystems. Other studies of $\delta^{13}C$ distribution have focused predominantly on benthic-pelagic coupling (Davenport and Bax 2002, Takai et al. 2004, Sherwood and Rose 2005, Vizzini

and Mazzola 2005) or between marine, estuarine and freshwater ecosystems (Haines and Montague 1979, Fry and Parker 1979, Wainright et a. 1996, Lee 2000, Doi et al. 2005) where very strong gradients in $\delta^{13}C$ exist. Our study was limited to the horizontal distribution in $\delta^{13}C$ of the dominant pelagic species at various trophic levels in the NCC, and did not examine many of the benthic and epibenthic species that likely interact with the pelagic environment (e.g. pandalid shrimp, Pacific hake, flatfishes, and adult rockfishes). Additional study of the degree of benthic-pelagic coupling in this system is warranted.

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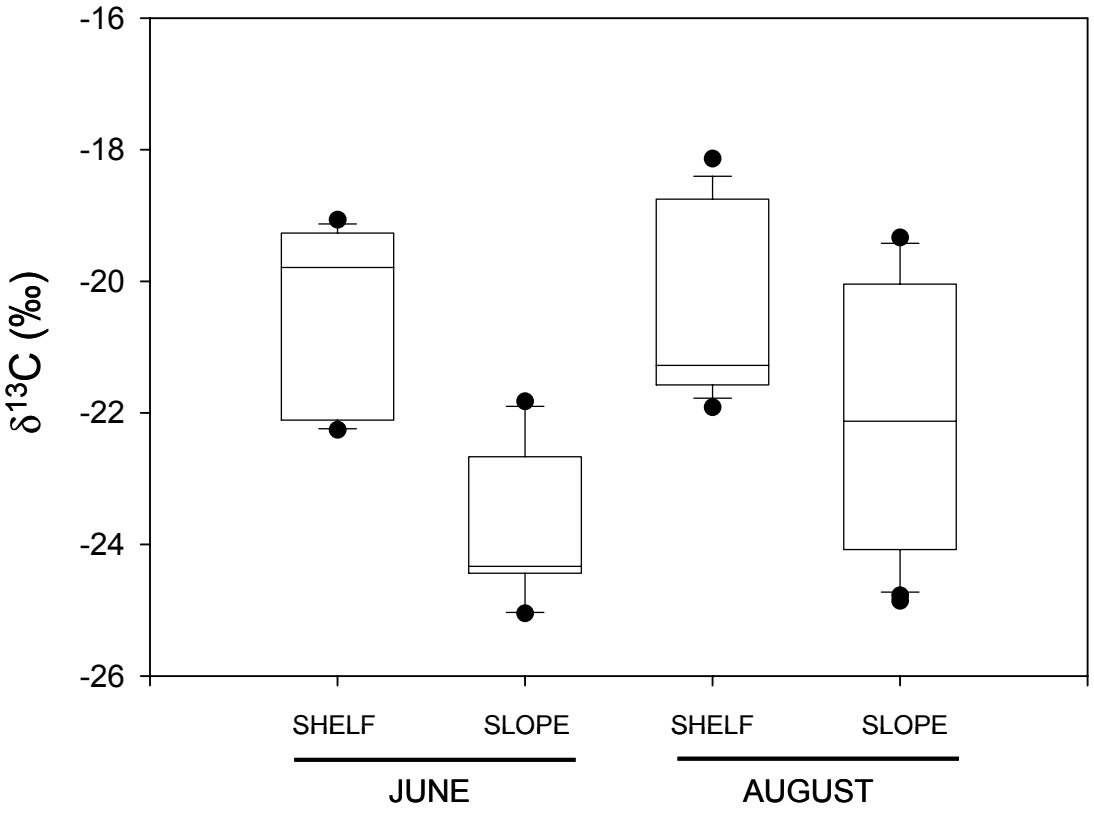

Figure 4.1. δ13C of particulate organic matter (POM) samples from shelf (depth <150m) and slope (>150m) waters collected during June and August 2002. Boxes denote 75% interquartile values, median (line). Vertical lines denote upper (97.5%) and lower (2.5%) data values with outilers (dots) being beyond this range.

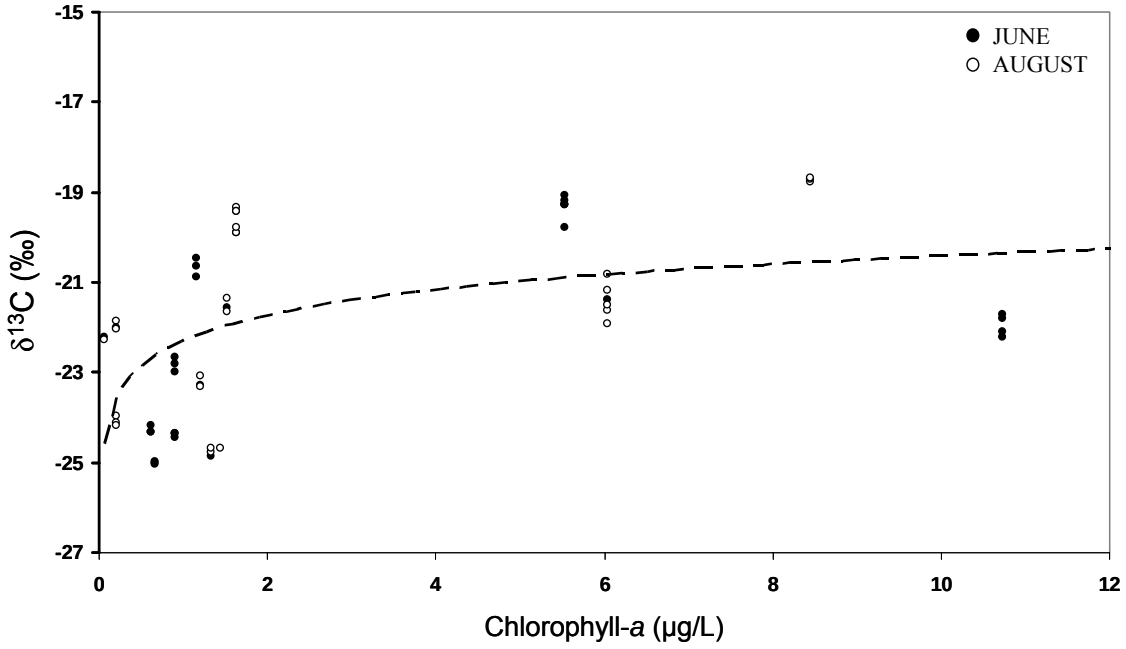

Figure 4.2. Relationship of δ13C and chlorophyll-a from June and August 2002 samples collected between Northern California and Washington. Least squared line is from both months combined using the following equation $\delta^{13}C = 0.82\ln(\text{chl-a})-22.3$ ($r^2 = 0.31$).

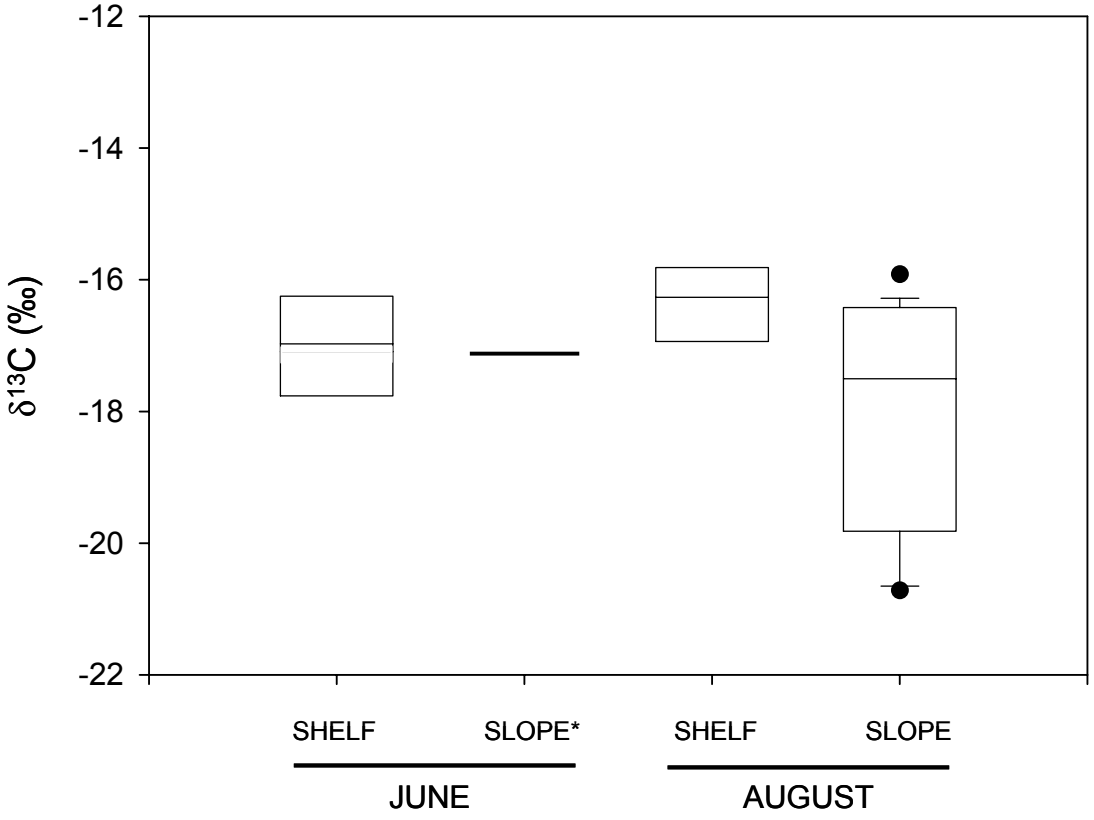

Figure 4.3. δ13C of copepods from shelf (depth <150m) and slope (>150m) waters collected during June and August 2002 cruises. June slope values only represent the mean due to a sample size of n=2. Boxes denote 75% interquartile values and median (line). Vertical lines denote upper (97.5%) and lower (2.5%) data values with outilers (dots) being beyond this range.

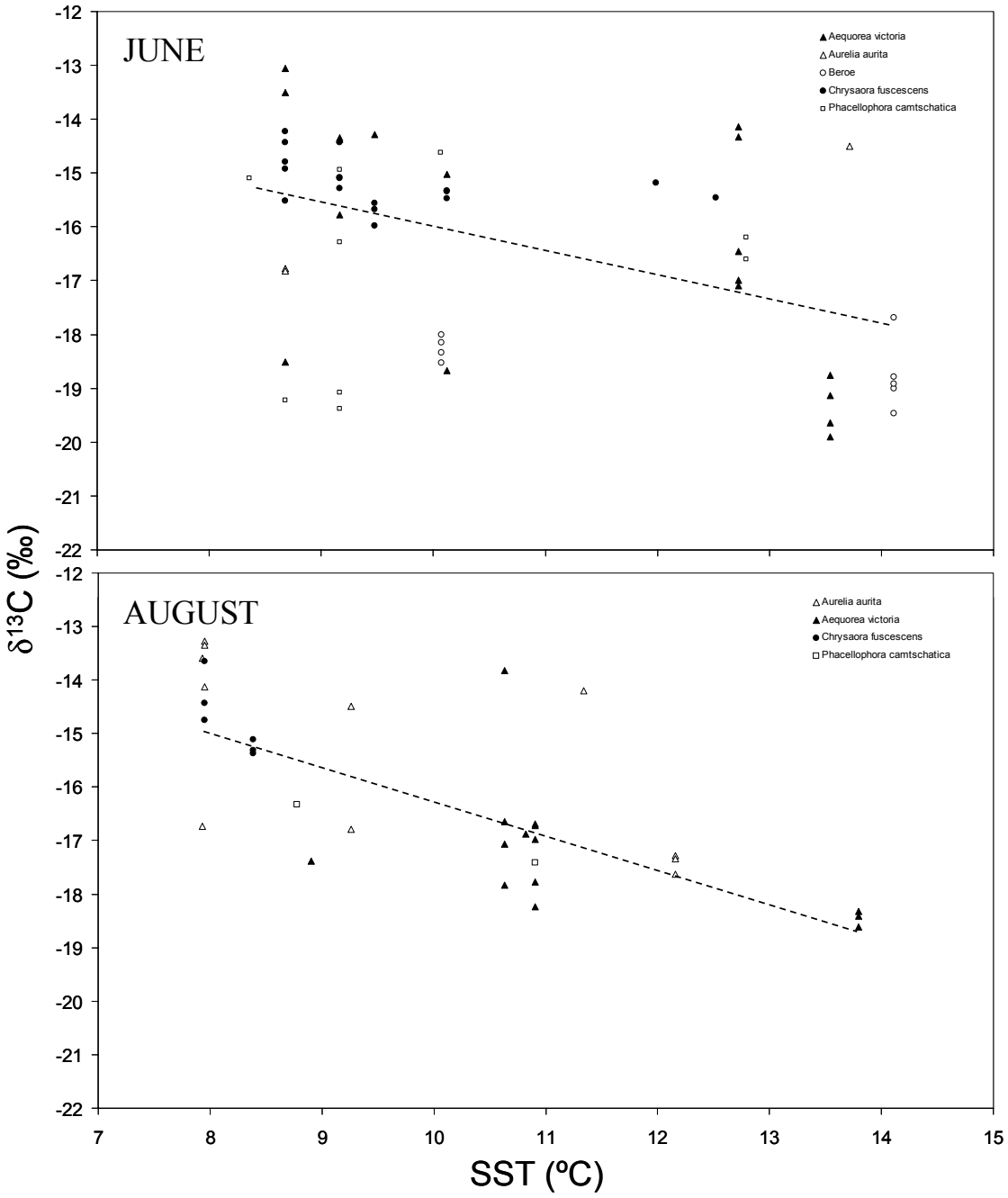

Figure 4.4. $\delta^{13}C$ of gelatinous zooplankton at varying sea surface temperatures (SST) collected during June (top) and August (bottom) 2002.

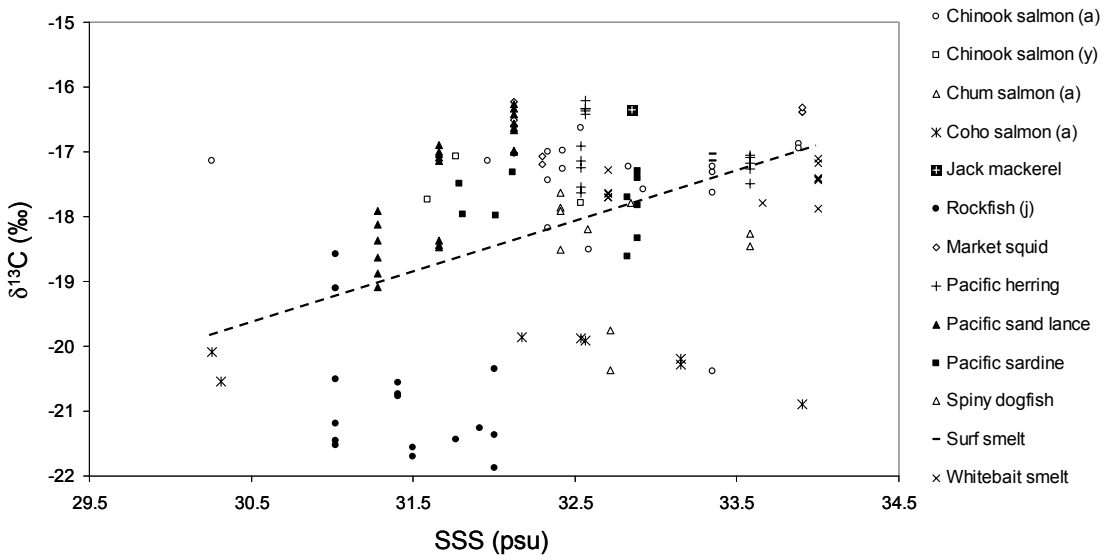

Figure 4.5. $\delta^{13}C$ of nekton species at varying sea surface salinities (SSS) collected during June 2002(r^2=0.15).

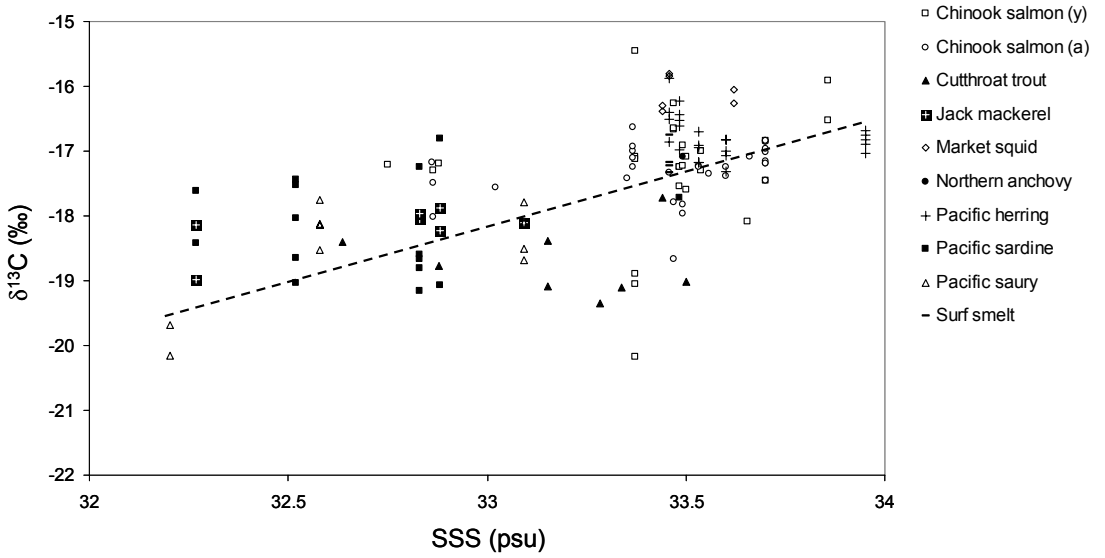

Figure 4.6. $\delta^{13}C$ of nekton species at varying sea surface salinities (SSS) collected during August 2002 (r^2=0.42).

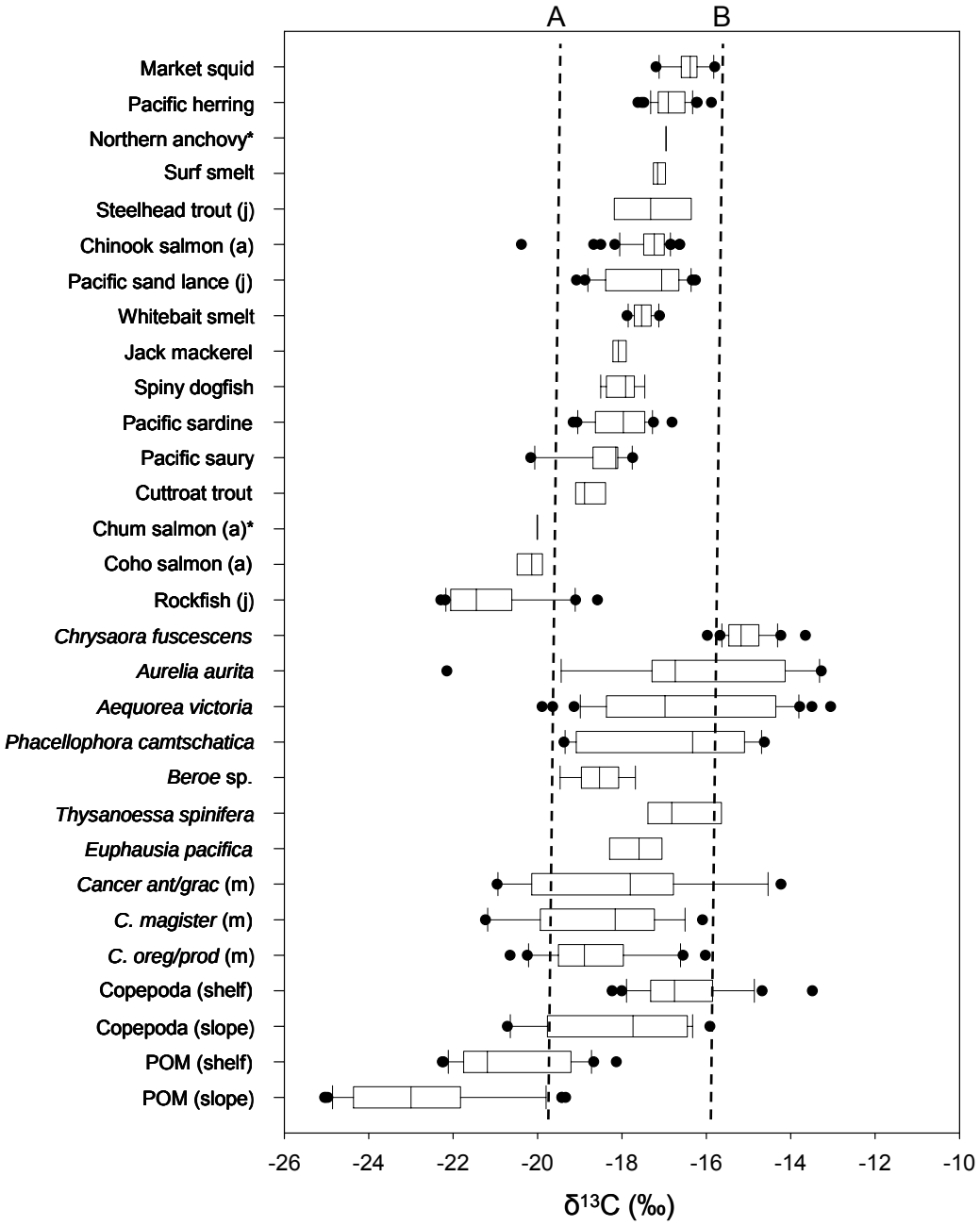

Figure 4.7. δ13C of zooplankton and nekton community from June and August 2002 combined. Boxes denote 25 and 75% interquartile values and median (line). Dashed lines A and B represent probable slope and shelf isotope signatures of copepods, respectively.

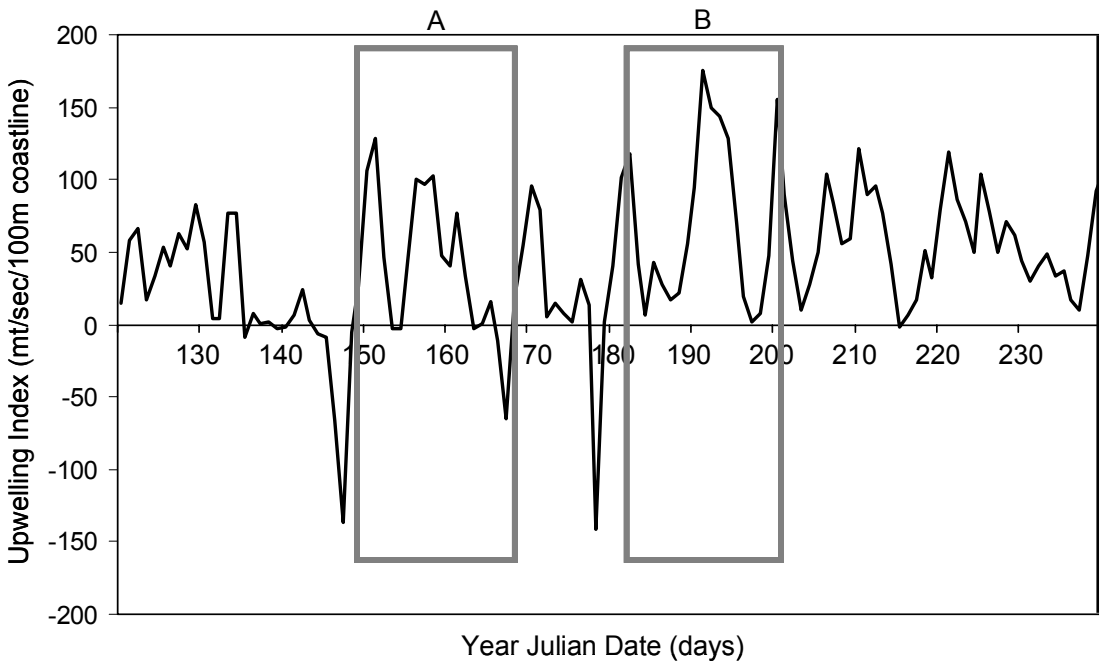

Figure 4.8. Daily upwelling index (45ºN 125ºW, Pacific Fisheries Environmental Laboratory, US National Oceanic and Atmospheric Administration) during 2002. Boxes denote the two GLOBEC cruise periods: 29 May – 18 June (A) and 29 July – 18 August (B).

CHAPTER 5

TISSUE-SPECIFIC RESPONSE OF $\delta^{15}N$ IN ADULT PACIFIC HERRING (*Clupea pallasi*) FOLLOWING AN ISOTOPIC SHIFT IN DIET

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ABSTRACT

The objective of this study was to measure the tissue-specific response of isotope $\delta^{15}N$ to changes in isotopic signature of diet in an adult marine fish (Pacific herring, *Clupea pallasi*), and to examine the importance of growth and metabolism in this shift. This was accomplished by maintaining wild adult Pacific herring in captivity and monitoring isotopic shift in tissues following a corresponding isotopic shift in diet, and the application of a metabolism/growth mixing model. Tissues examined were blood, eye, heart, liver, and white muscle. One group of herring was given a $\delta^{15}N$ diet depleted by approximately 5.4 ‰, and another given a ^{15}N-enriched diet labeled with 98 atom% l-phenylalanine. This study showed that (*i*) isotopic response of individual tissues following an isotopic shift in diet varied in both rate of change and fractionation level, (*ii*) most of this isotopic shift is due to growth, and (*iii*) white muscle and liver tissue appeared the most responsive to isotopic shift in diet, reaching isotopic equilibrium with diet in a matter of months (not years). These results indicate that the optimal period for measuring $\delta^{15}N$ in Pacific herring to observe trophic patterns in the field should occur after much of the summer growth period.

INTRODUCTION

Stable isotopes of carbon and nitrogen are commonly used in ecology to elucidate trophic patterns and source production (Rau et al. 1983, Vander Zanden et al. 1999, Post 2002), and are based on the fundamental assumption that isotopes are temporally integrated within an organism from its food source (O'Reilly et al. 2002). Isotopic integration is expressed as an organism's 'memory' (Harvey et al. 2002) of past feeding behavior. Temporal integration is attributed to physiological processes of growth (protein synthesis) and metabolic tissue replacement (turnover), yet the significance of each may be dependent on organism thermoregulatory strategy (Herzka & Holt 2000, McCutchan et al. 2002), physiological condition (Hobson et al. 1993, Fantle et al. 1999, Schmidt et al. 2004), and life history stage (Genner et al. 2003). For aquatic poikilotherms, such as

fish, the temporal integration of isotopes has been examined in larval-juvenile stages where isotopic shift was almost exclusively due to growth rather than metabolic turnover (Hesslein et al. 1993, Bosley et al. 2002, Harvey et al. 2002). However, no examination of slower-growing adult stages, those exhibiting rates below 0.001 $g \cdot d^{-1}$, has been performed where metabolic processes may be more significant in deriving temporal integration. Knowledge of isotopic integration is essential for providing a level of confidence that a particular signature provides a temporal measure of feeding behavior (O'Reilly et al. 2002) or for retention of a signature as a tracer of organism movement (Wassenaar & Hobson 2000).

Application of stable isotopes are based on the differential retention or loss of the heavier isotope (^{15}N) over the lighter (^{14}N) by an organism, termed fractionation (for review see Michener and Schell 1994). In biological systems, nitrogen isotopes are typically used to measure relative trophic level, observed as the signature of food source plus some fractionation level (around +3.4 ‰)(Post 2002). Knowledge of isotopic integration within an organism has significant implications for interpretation of field results, such as tissue-specific rates of change as a measure of 'recent' and 'longer-term' diet (Tieszen et al. 1983, Hobson & Clark 1992, Hesslein et al 1993, Lorrain et al. 2002), interpretation of temporal variation (Harvey & Kitchell 2000), distinguishing signature retention for migratory species (Fry 1981, Hesslein et al. 1991, Hansson et al. 1997, Fry et al. 1999, Hobson and Bairlein 2003) and organism condition (Hobson & Clark 1992, Hobson et al. 1993). For terrestrial homeotherms isotope turnover of nitrogen provides a fairly recent (within 10 d) indication of feeding behavior (Tieszen et al. 1983, Hobson & Clark 1992). Different tissues have shown different turnover rates, providing a 'clock' (Hesslein et al. 1992) of trophic shift (Hobson & Welch 1992). However, for aquatic poikilotherms temporal integration of nitrogen stable isotopes are less clear. Isotopic integration may be dependent on trophic level (O'Reilly et al. 2002), growth, and temperature (MacAvoy et al. 2001, Bosley et al. 2002). Of the studies measuring isotopic integration in aquatic poikilotherms, all have focused on fast-growing organisms, such as crustaceans (Fry & Arnold 1982, Frazer et al. 1997), fish larvae (Vander Zanden et al. 1998, Bosley et al.

2002, Herzka & Holt 2000, Tominaga et al. 2003), juveniles (Hesslein et al 1993, MacAvoy et al. 2001, Harvey et al. 2002), or fast-growing adults (Gaye-Siessegger et al. 2004). In all instances isotopic shift was predominantly due to added tissue growth. Although experiencing indeterminant growth, slower growing adult species of fish may experience turnover rates more attributed to metabolic processes (Fry & Arnold 1982, Maruyama et al. 2001). To date no study has examined turnover rates of $\delta^{15}N$ in an adult fish species exhibiting low rates of growth.

This study examines the tissue-specific response of stable isotope $\delta^{15}N$ to an isotopic shift in diet within adult Pacific herring (*Clupea pallasi*). This was accomplished by placing wild adult Pacific herring in captivity, and monitoring the tissue-specific isotope shift over time following switch to an isotopically different diet. Another approach was taken using a diet artificially labeled with a 98 atom% ^{15}N-enriched amino acid and observing the tissue-specific response over time. Non-labeled $\delta^{15}N$ diet was used to measure the approximate 'window' of past feeding activity and the relative contribution of metabolism and growth to isotope shift; artificial ^{15}N-labeling of diet allowed for a short-term observation of tissue-specific response and the dynamics of ^{15}N-pooling within the body. Pacific herring are ideal for this study for several reasons: they are ecologically significant as pelagic predators and prey in the North Pacific, are active swimmers with presumably high metabolic demands, and they acclimate well to captivity.

METHODS

Pacific herring were collected from Yaquina Bay, Oregon, USA, on 3 March 2002 (Julian date 59), using a commercial purse seine. Live fish were initially transported to a 3.66 m diameter x 1.5 m outdoor tank and allowed to acclimate for 10 d. Each fish was then lightly anesthetized with an MS-222 solution (30 $g \cdot ml^{-1}$), measured for wet weight, and individually tagged with a 1.1 × 0.25 mm sequential numerical coded wire tag (CWT). Tag identifiers allowed for measurement of individual growth of fish. Fish were then randomly assigned to one of six outdoor tanks (1.85 m diameter x 0.90 m, flow 15

$L \cdot min^{-1}$ using a sand filtered flow-through system from a marine source; mean temperature 10.6°C ± 1.6), with 50 fish per tank. Three tanks were randomly assigned to receive a non-enriched diet ($\delta^{15}N$ = 8.0‰ ± 0.87) and three a $\delta^{15}N$-enriched diet at a later period (0.875 atom % ± 0.003). Mean standard length of fish within this study were 169 mm (± 16.9), being an age of approximately 2-3 yrs (Hart 1973).

Non-enriched

Fish were given a non-enriched diet throughout the duration of the study by batch-feeding; however, fish generally did not start feeding after collection until Julian date 91. Throughout the study feeding was adjusted to maintain approximately 2.5% of dry body weight of food per fish per day; body weight was estimated from mean weight of fish from each sample period. A diet of approximately 50% protein was produced using fishmeal, commercial salmon feed and krill. Contents were blended together in liquid form, and solidified with the addition of food gelatin. Upon field collection, five fish were sampled for isotope analysis of tissues eye, heart, muscle and liver (blood was sampled later in the experiment only). Afterward, samples were collected at Julian day 137, 148 and thereafter every 30 d (5 sampling events). Because sampling missed the period when herring began to feed on the control diet, mean isotope values for this period were estimated by the combined mean of time of collection and the first sampling in captivity (Julian date 59 and 137, respectively). Comparison of tissue-specific $\delta^{15}N$ between the two sampling periods showed no significant difference (t-test, $p > 0.80$). The date of initiated feeding was then used to obtain absolute rate change of isotope values over time.

During the laboratory experiment, three fish were generally sampled from each tank; a notable exception to this occurred on date 241 when sampling was reduced to prolong the duration of the experiment. Upon collection, fish were euthanized using an overdose of $CaCO_3$-buffered MS-222 solution, and then measured for wet mass, and sampled for blood using a 3 cc syringe. All fish tissues were frozen for processing at a later period. Frozen tissues removed from Pacific herring were lightly rinsed with distilled water to

remove any extraneous material, oven-dried (80°C) for 36 hr and pulverized using a mortar and pestle. Stable isotopes were measured by calculating the ratio of the heavy to light isotope and comparing to a known standard, a commonly used equation that is provided in previous stable isotope literature (e.g., Fry & Arnold 1982, Tieszen et al. 1983, Michener and Schell 1994). Samples were analyzed for $\delta^{15}N$ at the University of Texas at Austin Marine Science Institute using a Carlo Erba Elemental Analyzer 2500 coupled to a Finnigan MAT Delta Plus stable isotope ratio mass spectrometer via a ConFlo-III continuous flow interface (measurement error ± 0.3‰).

Growth/metabolism model

The rate change of stable isotope $\delta^{15}N$ within a particular tissue is a function of growth (added tissue) and metabolic tissue replacement (Hesslein et al. 1993). This study estimated changes in $\delta^{15}N$ from growth and metabolic tissue replacement by applying a model previously used by Hesslein et al. (1993), MacAvoy et al. (2001) and Sakano et al. (2005). The following series of equations were applied:

(1) $C = ((W_o \cdot C_o) + ((W - W_o) \cdot C_n))/ W)$

Where C denotes the delta value of a fish at any time between its initial food (C_o) and new food (C_n). Initial and final weights of fish are represented as W_o and W respectively. Applying the growth model $W = W_o \cdot e^{kt}$ where *k* represents the per day growth rate and *t* the time (d), the growth rate *k* can then be solved as $k = \ln(W/W_o)/t$. Therefore, the following differential equations were used to denote change in C due to growth (eqn. 2, below) and metabolic tissue replacement (eqn. 3, below) separately:

(2) $dC/dt = -k \cdot (W/W_o) \cdot (C_o - C_n)$,

(3) $dC/dt = -m \cdot (C - C_n)$,

where *m* is the metabolic tissue replacement rate. Solving for the two equations provides the following combined model:

(4) $C = C_n + (C_o - C_n) \cdot e^{-(k+m)t}$,

where W_o is initial and W the final weights of a fish, and C, C_o, and C_n, represent measured $\delta^{15}N$, the $\delta^{15}N$ at equilibrium with old diet, and $\delta^{15}N$ at equilibrium with new diet, respectively. The contribution of metabolic turnover (*m*) to isotopic shift was

estimated using least squares regression, by regressing C over time to obtain the slope (*k* + *m*) and subtracting the growth component (*k*) to obtain a value for metabolic replacement. The value *k* varies according to individual growth rates obtained through laboratory measurements and eqn. 2, whereas *m* remains constant within individual tissues. The relative contribution of metabolic turnover and growth to isotopic shift was then measured by comparing regression r^2 values of the measured $\delta^{15}N$ and the predicted (eqn. 4) model containing the growth and metabolic component, and with growth only.

Enriched

On Julian date 137, enriched fish were given the ^{15}N-labelled diet for 10 d, and then switched to the control diet for the remainder of the study. Feeding regimen and diet were the same as control fish, with the exception that the enriched diet contained 98+ atom % ^{15}N l-phenylalanine. Sampling frequency during the initial 10 d enrichment period occurred at 8 and 24 h following the first feeding of enriched diet, and 6 and 10 d during the enrichment period. After 10 d, sampling frequency followed the same dates as the control fish. Sampling for enriched fish followed the same procedure as control fish with the exception that tissues were analyzed for $\delta^{15}N$ at the Oregon State University Department of Crop and Soil Science Stable Isotope Research Unit using a PDZ Europa Hydra 20/20 Isotope Ratio Mass Spectrometer (PDZ Europa, Northwich, Cheshire, UK)(± 0.2‰).

Because fish were batch-fed a ^{15}N-enriched diet, individual variation in food uptake may be expressed as variation in total tissue-specific enrichment. To account for this, the response of individual tissues to enrichment was standardized by obtaining the percent enrichment of each tissue within each fish. From all individuals within a sampling period, the relative (percent) enrichment (δE_i) for each tissue within a fish was obtained using the following equation:

$$(5) \quad \delta E_i = \left[\frac{\delta^{15} E_i}{\sum_{j=1}^{n} \delta^{15} E_j} \right] \times 100 ,$$

where *i* is one of *n* different tissues within an individual fish.

Data analyses

To examine potential tank and interactive effects on $\delta^{15}N$, multifactor analysis of variance (ANOVA) was performed with sample date, tank, and date x tank. Enriched tissues showed no significant effects, however after accounting for date and interaction terms, a moderate tank effect was observed in non-enriched $\delta^{15}N$ of blood ($p = 0.018$), eye ($p = 0.038$), liver ($p = 0.022$), and muscle ($p = 0.014$) tissue. Comparison of estimated means and confidence intervals from the multifactor and one-factor ANOVA with sample date as the single parameter showed very little difference between the two. It was therefore reasonable to pool data between tanks to perform linear regression methods without accounting for tank effect.

Linear regression was used to examine the dependence of $\delta^{15}N$ (non-enriched and enriched) on time (sample date), and to compare the slopes and intercepts between tissues. For each tissue parameter selection was performed using the original model of isotope value as a function of sample date, and sequentially adding second and higher order parameters of sample date until a satisfactory fit to the model was obtained. The best-fitted model was determined using a combination of Bayesian Information Criteria (BIC) and lack of fit F-test. BIC was used to compare a model to one with a higher order parameter. Where BIC was less objective, the lack of fit F-test was applied to examine the significance of retaining or dropping a higher order parameter. For non-enriched fish, comparison of intercepts and slopes of individual tissues with identically ordered parameters was performed using analysis of covariance (ANCOVA). First-order linear responses were compared directly through ANCOVA, whereas polynomial responses were compared using extra sum-of-squares F-test (ESS_F).

RESULTS

Non-enriched

Muscle and liver experienced a distinct shift (third-order polynomial) toward the lower $\delta^{15}N$ of diet after sample date 137, reaching equilibrium relative to food by day 210 (Fig. 5.1, Table 5.1). Liver and muscle polynomial regressions were significantly different in slope (ANCOVA; $ESS_{F[4,126]} = 17.7$; $p < 0.0001$) but not in absolute values (ANCOVA, $p = 0.09$) (Table 5.2). From the time of first feeding to equilibrium with diet, rate of isotope change for muscle and liver tissues were significantly different (ANCOVA, $p = 0.02$); 0.015 and 0.033‰ · d-1, respectively. After reaching equilibrium, mean $\delta^{15}N$ of muscle and liver were significantly different ($p < 0.0001$), with muscle being 5.1‰ and liver 3.7‰ fractionated from diet.

Tissues eye, blood and heart did not reach equilibrium with diet, however a linear (first-order) movement toward diet $\delta^{15}N$ was observed through the study period (Fig. 5.1, Table 5.1). Between time of first feeding and the remainder of the study (d 302), the rate of change of heart, blood and eye $\delta^{15}N$ were estimated to be 0.022, 0.023, and 0.005‰ · d^{-1}, respectively. Regression slope of eye $\delta^{15}N$ was significantly lower than that of blood and heart (both $p < 0.0001$); blood and heart were not significantly different from each other ($p = 0.10$, respectively). Fractionation among tissues from diet varied, with heart slightly more fractionated than blood (mean = 0.39‰ ± 0.16), and heart and blood being significantly different from eye (mean = 0.79‰ ± 0.16 and 1.17‰ ± 0.16, respectively, both significantly different $p < 0.0001$). By the end of the experiment (d 302) fractionation of eye, blood and heart tissues from diet were 3.4, 4.7 and 4.9‰, respectively.

Growth/metabolism model

Model predictions of $\delta^{15}N$ based on growth ($k = 0.0007$ g · d^{-1}) and metabolic turnover contribution to isotopic shift varied among tissues, with muscle and liver tissues having the best fit to measured data ($R^2 = 0.63$ and 0.57, respectively), followed by blood (0.22), heart (0.17), and eye (0.01). For tissues muscle and liver, growth accounted for just over

half of the variance explained ($R^2 = 0.35$ for both). Estimated values for metabolic tissue replacement were relatively high for heart ($m = 0.01‰ \cdot d^{-1}$) and muscle ($0.007‰ \cdot d^{-1}$) tissue, moderate for blood ($0.0004 ‰ \cdot d^{-1}$) and liver ($0.0004 ‰ \cdot d^{-1}$), and very low for eye ($-0.02 ‰ \cdot d^{-1}$) tissue.

Enriched

Feeding of the $\delta^{15}N$-enriched diet by Pacific herring was followed by a rapid increase (within 8 hr) in $\delta^{15}N$ within liver (mean 156.4‰ ± 63.2), blood (49.6‰ ± 19.9), heart (49.2‰ ± 18.0), and muscle (28.6‰ ± 5.8), with a slight increase in eye tissue (18.4‰ ± 3.6) (Figure 5.2a and 5.2b); mean values of $\delta^{15}N$ for non-enriched fish never exceeded 17.0‰. After 10 d of ^{15}N-enriched diet, the level of $\delta^{15}N$ varied among tissues; liver increased the most (926.8 ‰ ± 469.8), followed by blood (461.7‰ ± 302.7), heart (285.2‰ ± 151.6), muscle (142.1 ‰ ± 73.5) and eye (75.1‰ ± 33.3) tissue. The switch from enriched to control diet after 10 d enrichment, and subsequent sampling between 33 and 155 d post-enrichment showed a significant drop in liver and blood $\delta^{15}N$, and a steady drop in heart, muscle and eye tissue $\delta^{15}N$ (Table 5.3) (Figure 5.2a). Relative enrichment of tissues within individual fish (eqn. 5) over time revealed pooling and release of $\delta^{15}N$ through tissues. The liver remained the most enriched tissue through the 10 d enrichment period, but $\delta^{15}N$% dropped precipitously after sample day 43, while other tissues continued to gradually increase in relative enrichment (Figure 5.2b).

Table 5.1. Laboratory experiment data from tissue-specific measures of $\delta^{15}N$ over time of captive Pacific herring (*Clupea pallasi*) given an isotopically different diet (mean diet $\delta^{15}N = 8.0‰ \pm 0.87$).

Time	n	Blood	Eye	Heart	Liver	Muscle
59[a]	5	-	11.9 (0.8)	14.9 (0.4)	13.1 (0.6)	13.8 (0.4)
137	10	14.1 (0.8)	11.7 (0.4)	14.4 (0.9)	14.0 (0.9)	14.0 (0.5)
148	8	13.1 (0.7)	11.0 (0.4)	14.7 (0.5)	13.8 (0.8)	13.8 (0.5)
180	9	13.0 (0.8)	11.6 (0.3)	14.3 (0.5)	12.8 (1.3)	13.6 (0.3)
210	9	12.2 (0.7)	10.9 (0.7)	12.8 (0.4)	11.3 (0.3)	12.8 (0.5)
241	6	13.3 (0.5)	11.4 (0.6)	12.8 (0.3)	11.8 (0.1)	13.1 (0.4)
272	9	12.2 (0.8)	11.3 (0.5)	13.1 (0.4)	11.4 (0.6)	12.6 (0.4)
302	9	12.1 (0.3)	10.9 (0.6)	12.5 (0.4)	11.0 (0.7)	12.5 (0.5)

[a] Time of collection

Table 5.2. Results from linear and polynomial regression of mean isotope composition ($\delta^{15}N$) as a linear function of Julian date from captive Pacific herring (*Clupea pallasi*) given $\delta^{15}N$ non-enriched diet (mean $\delta^{15}N$ =8.0‰±0.87).

Stable Isotope Tissue				**Model**		
Parameter	**Coefficient**	**SE**	**p-value**	**R^2**	**Model (Total) df**	**p-value**
$\delta^{15}N$						
Blood				0.390	1 (59)	<0.001
Intercept	15.179	0.378	<0.001			
Date	-0.011	0.002	<0.001			
Eye				0.105	1 (64)	0.009
Intercept	11.915	0.228	<0.001			
Date	-0.003	0.001	0.009			
Heart				0.588	1 (64)	<0.001
Intercept	15.90	0.253	<0.001			
Date	-0.01	0.001	<0.001			
Muscle				0.546	3 (65)	<0.001
Intercept	12.3	0.835	<0.001			
Date	0.038	0.017	0.024			
$Date^2$	$-2.5x10^{-4}$	$9.8x10^{-5}$	0.012			
$Date^3$	$4.2x10^{-7}$	$1.8x10^{-7}$	0.021			
Liver				0.595	3 (63)	<0.001
Intercept	9.3	1.439	<0.001			
Date	0.09	0.028	0.001			
$Date^2$	-0.006	$1.7x10^{-4}$	<0.001			
$Date^3$	$1.1x10^{-6}$	$3.1x10^{-7}$	<0.001			

Table 5.3. Tissue-specific δ15N enrichment of captive Pacific herring (Clupea pallasi). From Julian day 137.3 – 149.0 Pacific herring were given a ^{15}N-enriched diet (98 atom % l-phenylalanine, mean atom % $\delta^{15}N$ =0.875±0.003), then at Julian date 148 switched to a non-enriched diet (mean $\delta^{15}N$ =8.0‰±0.87) through the remainder of the study.

			Tissue-specific $\delta^{15}N$ ‰ mean (±SD)				
Julian Date	**Diet type**	**N**	**Blood**	**Eye**	**Heart**	**Liver**	**Muscle**
137.3	Enriched	9	49.6 (19.9)	18.4 (3.6)	49.2 (18.0)	156.4 (63.2)	28.6 (5.8)
138.0		7	45.3 (43.8)	15.4 (4.4)	35.3 (19.6)	111.5 (92.7)	25.6 (12.3)
143.0		9	230.5 (205.3)	45.0 (21.8)	145.9 (92.3)	577.1 (373.2)	85.0 (49.9)
148.0	Non-enriched	9	461.7 (302.7)	75.1 (33.3)	285.2 (151.6)	926.8 (469.8)	142.1 (73.5)
180.0		9	384.1 (261.8)	80.8 (16.5)	271.3 (86.8)	439.6 (98.8)	156.6 (50.6)
210.0		9	305.5 (292.6)	54.9 (25.4)	189.1 (133.8)	172.3 (95.9)	104.1 (63.3)
241.0		5	158.5 (111.8)	113.4 (83.6)	136.8 (71.3)	72.0 (50.4)	124.4 (65.2)
272.0		9	136.4 (104.0)	48.9 (18.9)	113.7 (56.7)	84.7 (36.3)	110.9 (57.4)
302.0		10	184.7 (140.6)	44.7 (13.7)	127.8 (56.2)	89.3 (38.5)	109.1 (40.3)

DISCUSSION

This study provides the first measure of tissue-specific changes in $\delta^{15}N$ within an adult marine pelagic fish (Pacific herring, *Clupea pallasi*) and fills an important gap in the examination of temporal integration of isotopes in a slower-growing, yet highly active species. Results indicate that tissues differ in their isotopic response to an isotopic shift in diet, and that these differences are expressed in terms of rate shift and fractionation level from diet. Measures of isotopic integration and the influence of growth and metabolism in Pacific herring furthermore provide an estimate of the optimal period to measure $\delta^{15}N$ in this species to examine trophic activity of interest.

Non-enriched

Liver and muscle reached isotopic ($\delta^{15}N$) equilibrium during the study, whereas blood, eye and heart continued toward equilibrium throughout the experiment. Liver and muscle tissue may therefore provide the most recent measure of feeding activity (rate change 0.033 and 0.013‰ · d-1, respectively). Hesslein et al. (1993) estimated a substantially longer period to equilibrium (> 1 yr) in broad whitefish, and Harvey et al. (2002) estimated a threefold increase in mass in lake trout before reaching isotopic equilibrium with diet (within at least 100 d). Mean growth rates of Pacific herring here were very small (0.0007 g · d-1), with fish increasing in mean mass by only 1.3% (± 0.17) by the time isotopic equilibrium was reached in muscle and liver. Because isotopic shift is a function of metabolic and anabolic activities (Hesslein et al. 1993, MacAvoy et al. 2001, Harvey et al. 2002, Witting et al. 2004), the difference in growth contribution relative to isotopic shift presented here may be indicative of higher turnover rates in Pacific herring (discussed later in Model estimates) compared to that observed in other studies (e.g., Hesslein et al. 1993, MacAvoy et al. 2001, and Harvey et al. 2002).

Variation in fractionation and small differences in turnover among tissues is a fundamental limitation to effective use of multiple-tissue studies in poikilotherms. Use of isotopes of multiple tissues as a ‘clock’ of past and recent feeding in poikilotherms by

Hesslein et al. (1993) and MacAvoy et al. (2001) showed very small differences in rate change between muscle and blood (respectively), tissues commonly used to represent 'slow' and 'fast' tissues in homeotherms (e.g., Hobson et al. 1993, Doucett et al. 1999, Dahl et al. 2003). Pacific herring also displayed very small isotopic differences between liver and muscle in $\delta^{15}N$. On the other hand, $\delta^{15}N$ shift in eye tissue was distinctly slower than in other tissues, and may provide the clearest difference for delineating a 'fast' versus 'slow' tissue. Of the 'fast' tissues observed, muscle provided the most consistent $\delta^{15}N$ values and responded quickly to isotopic shift in diet. Pinnegar & Polunin (1999) observed the same characteristics in white muscle and suggest its use over other tissues. Another muscle-based tissue, such as heart, displayed similar qualities and may be useful in isotopic studies. An advantage of white muscle over heart tissue is the ease of extracting ample amounts of tissue and the absence of blood that has to be thoroughly rinsed from heart. Dorsal muscle is furthermore recommended because of its wide use in other studies.

Fractionation of $\delta^{15}N$ in tissues varied in Pacific herring, with muscle tissue being the most fractionated, followed by heart, blood, liver and eye. Fractionation among tissues was likely due to the differential allocation of proteins and amino acids among tissues, termed isotopic routing (Gannes et al. 1997). Isotopic routing has been well documented in other poikilotherms (Hesslein et al. 1993, Pinnegar & Polunin 1999, Lorrain et al. 2002) and homeotherms (Tieszen et al. 1983, Hobson & Clark 1992, Pearson et al. 2003). Muscle tissue is often observed more fractionated relative to other tissues and diet (Hesslein et al. 1993, Pinnegar & Polunin 1999, Johnson et al. 2002, Lorrain et al. 2002), however not to the extent observed here. Mean fractionation of muscle tissue over the period of equilibrium was approximately 5‰, roughly 1.6‰ greater than the "average" fractionation of 3.4‰ per trophic level (Post 2002). The basis of this may be due to diet or physiological processes involving higher turnover rates when growth is low. Higher protein-based diets have accounted for higher fractionation factors (Adams & Sterner 2000), which may have contributed to unusually high $\delta^{15}N$ fractionation values observed here. The percent nitrogen of food given Pacific herring was approximately 11.0%,

toward the higher end of %N of zooplankton (5.1-13.1%) (Omori 1969), typically consumed by wild Pacific herring (Foy & Norcross 1999). The increased $\delta^{15}N$ of tissues, particularly muscle, may also have been due to higher turnover rates. This has been typically observed in homeotherms where higher tissue turnover (due to catabolism) resulted in significant fractionation of $\delta^{15}N$. The influence of turnover in poikilotherms is not well understood, especially since most studies have focused on fast-growing species and life history stages where growth would override this effect. Frazer et al. (1997) measured no change in $\delta^{15}N$ of captive Antarctic krill (*Euphausia superba*) after fasting for two months, and Doucett (1999) observed no shift in $\delta^{15}N$ of muscle in migrating (fasting) Atlantic salmon (*Salmo salar*). However, some evidence suggests metabolic turnover may influence isotopic uptake in poiklotherms. Doucett (1999) also observed elevated $\delta^{15}N$ fractionation in liver of fasting *S. salar*, and blue crab (*Callinectes sapidus*) given low protein diets increased in muscle $\delta^{15}N$, perhaps due to catabolism of tissues (Fantle et al. 1999).

Metabolism/growth model

Added tissue growth accounted for most of the isotopic shift in diet, which is in general agreement with other studies of fish (e.g. Hesslein et al. 1993, MacAvoy 2001, Harvey et al. 2002, Sakano et al. 2005). However, fish within this study exhibited very little growth and reached equilibrium faster than previous studies. Direct comparison to other studies is problematic due to species and life history differences in growth, metabolism and temperature effects on both (Jobling 1994), where smaller fish exhibit higher metabolic demands (Kitchell et al. 1977, Jobling 1994) and require less growth to reach isotopic equilibrium with diet (Post 2002). Sakano et al. (2005) observed age-specific contribution of metabolism to isotopic shift in sockeye salmon (*Oncorhynchus nerka*), with age class 1+ fish having a higher metabolic contribution than age 3+ fish. Pacific herring in this study had a mean wet weight of 50.8 g (± 14.1) and exhibited only 1.3% increase in weight by the time isotope equilibrium was met. In contrast, Hesslein et al. (1993) using broad whitefish (*Coregonus nasus*), a colder water arctic-subarctic species, with a mean initial weight of 26g failed to reach equilibrium with diet after an approximate tenfold

increase in weight. Harvey et al. (2002), using captive lake trout (*Salvelinus namaycush*) with an average initial weight of 55g, simulated a threefold growth in weight between diet shift and reaching isotopic equilibrium. In view of this it is apparent that species may vary greatly in their isotopic shift relative to growth, and possibly metabolic processes. For Pacific herring metabolic turnover may play a more significant role in isotope turnover for two reasons: (a) Pacific herring used in this study were adults (between 2-3 yrs old), having lower growth rates compared to other studies examining juvenile stages (e.g. Hesslein et al. 1993, MacAvoy et al. 2001), and (b) Pacific herring are a highly active pelagic schooling fish with higher activity attributing to higher metabolic demands.

It is reasonable to assume that fish within this study were not identical to their wild counterparts. Fish failed to feed for 32 d after capture which may explain the relatively low growth rate observed. Total mortality of 12% was higher than desirable for the 148 d duration of this study, however much of this (92%) occurred 30 d prior to the onset of isotopic shift (Julian date 150). Also, the metabolic/growth model used here only provides a rough estimate of the influence of growth and metabolism to isotopic shift. Witting et al. (2004), examined the sensitivity of such models to growth and metabolism and conclude that it would take a metabolic demand >50% to statistically detect metabolic shift. For fish this is not likely to occur because they tend to have very low levels of protein degradation (i.e., tissue turnover) allowing for higher growth efficiencies (Carter et al. 1993, McCarthy et al. 1994). Other models applying a more refined tracer method would be required to establish the true contribution of turnover and growth.

Enriched

The goal of using a highly enriched $\delta^{15}N$ diet was to compare the isotopic response of individual tissues to a corresponding shift in dietary $\delta^{15}N$. The progression of ^{15}N-tracer among tissues observed in adult *Clupea pallasi* confirms the importance of isotopic routing and the unequal dispersal of ^{15}N among tissues. Rapid and significant uptake of ^{15}N occurred in blood and liver, with subsequent reallocation to muscle, heart, and eye. The general path of movement from intestinal absorption to organ systems of $\delta^{15}N$-l-

phenylalanine would have gone to the liver through portal blood (Smutná et al. 2002), and also directly to other tissues by amino acid routing (Gannes et al. 1997). Assimilation by liver would have furthermore released nitrogen as free amino acids into other tissue pools, such as muscle and blood, and eventually re-released into blood as metabolic ammonia (Smutná et al. 2002). This is confirmed by the relative (percent) increase in $\delta^{15}N$ of blood during enrichment and muscle following post-enrichment (Figure 5.2b), indicating the role of blood as a moderator among tissue-specific uptake and release of ^{15}N.

Other than this study, no known application of a $\delta^{15}N$-enriched amino acid through feeding and monitoring major tissues has been examined, although alternative delivery methods, such as direct injection ('flooding dose') and radioisotopes have been used (Mambrini & Guillaume 2001). Use of ^{15}N-l-phenalalanine as a tracer has been examined in whole body larval Atlantic halibut, *Hippoglossus hippoglossus* (Fraser et al. 1998), and Atlantic salmon (*Salmo salar*) smolts (Owen et al. 1999), both of which focused on growth efficiencies and protein synthesis. As with conventional isotopic analysis of whole tissue, more recent methods of compound-specific analyses are in need of refinement. Enrichment studies as the one presented here provide a framework for elucidating tissue-specific responses for a specific amino acid, and can be applied to specific compounds of interest. Recent advances in the analysis of stable isotopes of specific amino acids (e.g. Fantle et al. 1999, McClelland & Montoya, 2002, Schmidt et al. 2004) and fatty acids (e.g. Pond et al. 1998) may reveal a protein or amino acid that is not fractionated or is equally dispersed among tissues and could therefore be examined to determine tissue-specific responses over time.

Conclusions

Pacific herring muscle and liver tissue $\delta^{15}N$ reached equilibrium with diet in a matter of months (not years), with little growth having occurred. Growth however contributed to most of the isotopic integration of diet $\delta^{15}N$. For a species of fish exhibiting seasonal feeding and growth, the results presented here underlie the importance of sampling an

organism at an appropriate time to capture the range of isotopic integration. To observe trophic processes in Pacific herring measurement of isotopes should occur after much of the summer growth period (June-September).

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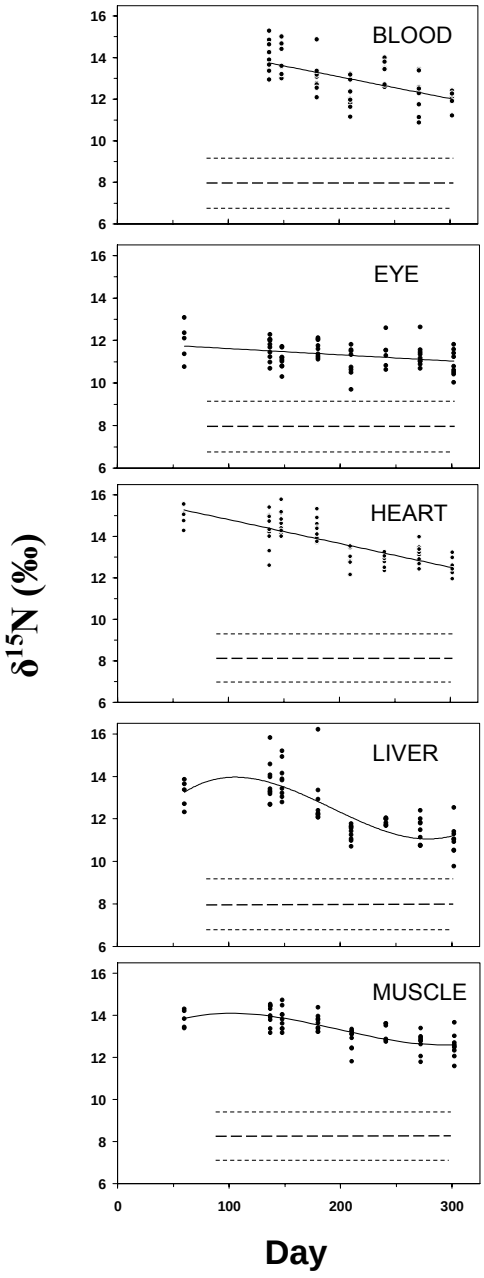

Figure 5.1. Plot of tissue-specific δ15N of captive Pacific herring (Clupea pallasi) given non-enriched diet (mean=8.0± 0.87‰) over time. Initial measures of $\delta^{15}N$ (Julian date 59) occurred during collection of fish, approximate time of first feeding of fish is indicated by the appearance of lines, delineating mean (**---**) and standard deviation (----) of diet (Julian date 91).

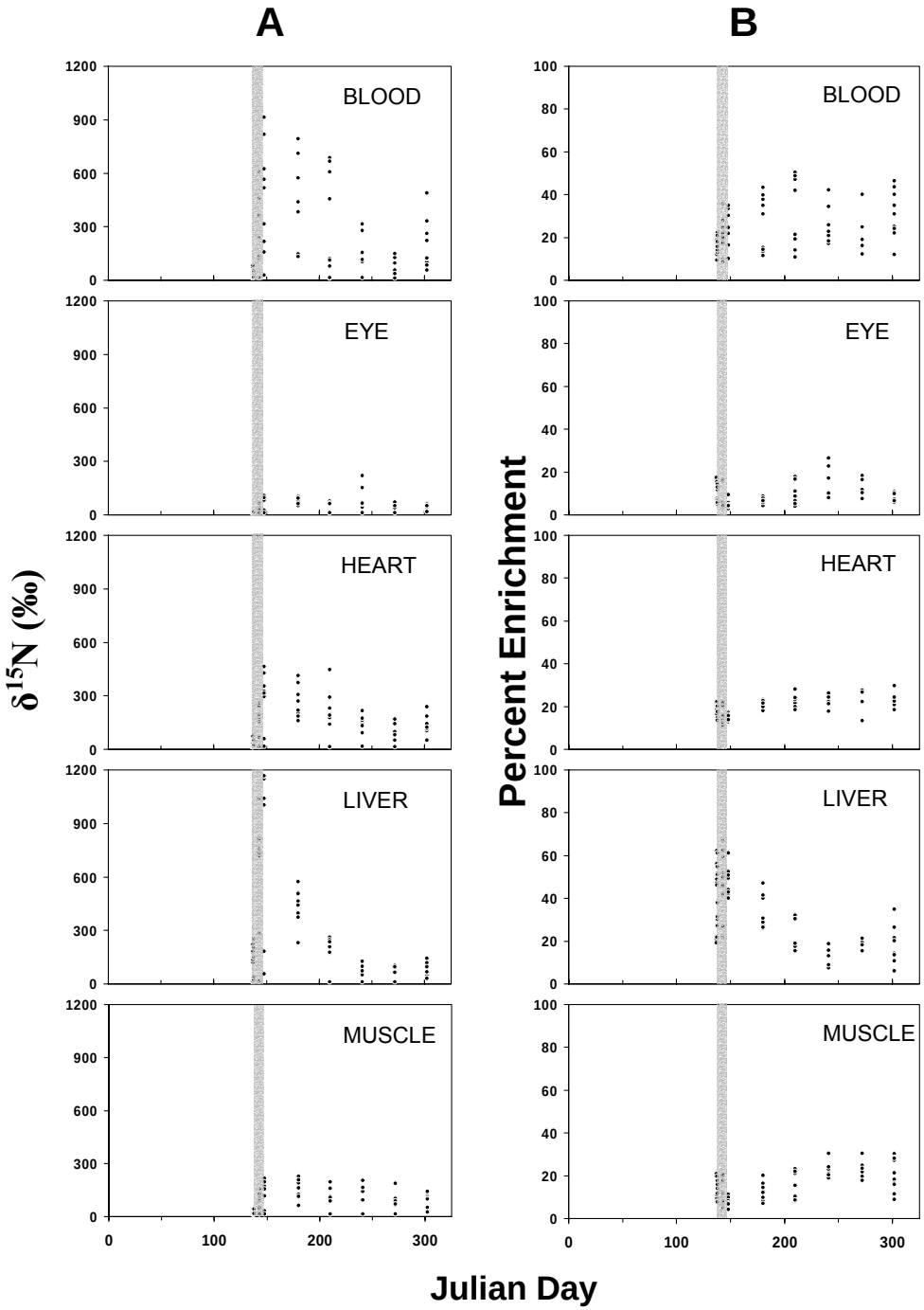

Figure 5.2. Plots of tissue specific 15N-enrichment in captive Pacific herring (Clupea pallasi) using (a) absolute values of δ15N, and (b) relative (%) δ15N-enrichment. Pacific herring were given a ^{15}N-labelled diet (mean atom %=0.875±0.003) for 10d (shaded region), and thereafter switched to a non-enriched control diet (mean δ^{15}N=8.0±0.87‰).

CHAPTER 6

Todd W. Miller

DISCUSSION

This dissertation provides the first comprehensive analysis of an EBC food web using diet and stable isotopes. From Chapter 2, analysis of nekton diets showed a food web consisting of high dietary overlap between many putative trophic levels (e.g. baitfish to adult sharks) and omnivory from top predators due to the consumption of euphausiids. This was confirmed from Chapter 3 results of $\delta^{15}N$ showing many supposed upper trophic level species (e.g. blue shark, jack mackerel) were feeding only at a marginally higher trophic level than baitfish and other species that primarily consumed euphuasiids. During the time of this study the NCC ecosystem exhibited anomalously high levels of upwelling and productivity (Wheeler et al. 2003), high ocean survival of salmonids, and increased abundances of baitfish and other nekton species (Peterson and Schwing 2003, Emmett et al. 2006). Brodeur and Pearcy (1992) observed a similar pattern of greater dietary overlap among nekton during relatively high production years during the 1980s. The pattern of less discrimination and greater dietary overlap has been observed in other aquatic (Michaletz 1997) and terrestrial systems (DuBowy 1988, Stevenson et al. 2000) and implies that production of a single or several abundant prey can be utilized across many species and trophic levels.

Within the NCC system it appears that, at least for some species, this level of dietary overlap may be spatially partitioned across the shelf. From Chapter 4, I observed a strong spatial gradient in cross-shelf enrichment of $\delta^{13}C$ in zooplankton and nekton that were associated with nearshore-offshore differences in primary production, indicating that direct competition between dominant nekton species is probably more dispersed across the shelf. This subdivision of the NCC system was in general agreement with Brodeur and Pearcy's (1992) assertion of the NCC food web having structure of nearshore, mid-shelf and offshore species. They further contend that interannual shifts in upwelling may cause shifts in the food web structure of the shelf-slope ecosystem. In Chapter 4, this was confirmed through the observation of a greater degree of $\delta^{13}C$ variability in offshore species of copepods and phytoplankton (POM), which likely resulted from advection of organisms across the shelf.

Interannual differences in the NCC food web appeared more variable than interdecadal variability (Chapter 2), as indicated by the lack of difference in prey consumed by juvenile and adult Chinook, juvenile Coho and jack mackerel analyzed from GLOBEC 2000 and 2002 cruises to collections and analysis from Brodeur and Pearcy (1992). Euphausiids and larval-juvenile fish were almost always the two most dominant taxa, with minor species varying from year to year. The apparent lack of difference between the two periods is contrary to assumed bottom-up forcing from a regime shift perspective, where abiotic factors cause shifts in primary production eventually leading to increased food for salmonids (e.g. Gargett 1997, Ware and Thomson 2005) and other nekton. Possibly the mechanisms at play are not reflected in diets at the time of our studies (i.e. late spring and summer months) and that the methods of dietary analysis alone, without including dimensions of predator and prey biomass, cannot reveal mechanisms of bottom-up or top-down patterns in the system. Moreover, if we examined dietary differences on a finer taxonomic resolution of prey, we might expect to see some differences not evident at the coarser scale applied. For example, among the prey larval-juvenile fish species we observed, we noted that sardines are a common prey during the time of our study whereas they were essentially absent in the 1980s (Emmett et al. 2006).

Bottom-up, top-down or wasp-waist control

This dissertation (Chapters 2 and 3) indicates the importance of primary (euphausiids, copepods and decapod larvae) and secondary consumers (larval fish and possibly euphausiids) to the dominant nekton within this system, suggesting some level of bottom-up control to mid-upper trophic level species (e.g. anchovy, sardine, smelts, herring and market squid). From the spatial coherence of chlorophyll-*a* values and resident fish species biomass, Ware and Thomson (2005) contend that the NCC system is regulated by bottom-up processes. During extreme El Niño and La Niña events, bottom-up processes are most apparent due to shifts in basal production and subsequent transfer to higher trophic levels (Pearcy and Schoener 1987, Brodeur and Pearcy 1992). Interestingly, Field et al. (2006) applied a simulation of the NCC ecosystem and observed significant

improvement to model predictions when using climate as a bottom-up (shifts in the Pacific Decadal Oscillation, PDO) and top-down (increase in warm-water predators) control. The top-down control Field et al. (2006) applied was from a warm/positive shift in the PDO causing a shift in the abundance and species composition of warm-water predators. I suggest that this is more a condition of bottom-up control where prey species are already compromised by lower productivity and the relative contribution of top-down control is enhanced by a shift in the predator-prey ratio. Furthermore, predators within this system, as well as in other EBC systems, appear too sparse to regulate the high number of mid-trophic forage fish within this system. The mechanism of wasp-waist control, at least in its formal definition of one or two dominant baitfish species placing top-down and bottom-up control within the system is not likely to be the main controlling force in the NCC. The amount of omnivory within the NCC would seem to dampen wasp-waist control by top predators bypassing the baitfish trophic level (Fig. 6.1). The only notable link between baitfish and upper trophic levels from this study was occasional consumption of juvenile pelagic rockfish by Pacific herring, smelt, and juvenile salmon (Chapter 2). Likewise, control of zooplankton by dominant nekton does not appear to be significant in this system. For example, Robinson (2000) failed to find a measurable impact of nekton (primarily hake and herring) predation on euphausiids off Vancouver Island.

In view of the three hypothesized processes controlling EBC ecosystems, it is likely that bottom-up control is most prevalent in the NCC, but that all three function to varying degrees and occur on different time scales, life history stages, and varying abundances of available prey. In a recent hypothesis to explain some of the ambiguities of "wasp-waist" control and differing time scales with respect to prey abundance, Bakun (2006) hypothesized predation on "wasp-waist" species (e.g. sardine and/or anchovy species) is low at low population numbers, but increased and is maximized at some intermediate level (termed the "predator pit") where predators have detected an abundance of prey. If prey (i.e. forage species) abundance continues beyond some saturation point where predators are satiated, the population then escapes the relatively high predation

experienced at lower population levels. Whether this occurs in any upwelling system is unknown and Bakun (2006) only provides hypothetical scenarios where this situation might occur. It is reasonable to assume that larval-juvenile fish experience some maximum predation level as numbers increase, after which then decreases due to prey saturation. Whether this forms the population "boom-bust" cycles in EBC ecosystems is questionable, in part because this is a highly simplistic view that assumes larval-juvenile fish abundance is independent of other available prey species. In the NCC system this dual species predator-prey interaction is not evident.

Stability, Complexity and Issues of Scale

The relatively low trophic diversity of the NCC pelagic food web coupled with strong trophic links from base production to primary and secondary consumers has significant implications with respect to ecosystem stability. As a general rule, more complex, diverse and highly-linked ecosystems are associated with greater general stability (McCann 2000), with stability defined as the population variance through time (McCann 2000). The strong links between basal production and low and mid-trophic levels observed here would suggest the system might be more susceptible to perturbations that carry through the food web. El Niño events are an extreme example of this where changes in abiotic factors can undermine basal production and food availability to higher trophic levels (Brodeur and Pearcy 1992). This perturbation differs from more decadal-scale shifts in productivity (e.g. PDO, Mantua et al. 1997), which may be a more gradual transition to a different equilibrium level.

Whether ecosystem stability is a function of the trophic links and strengths in this system is difficult to ascertain. As with relatively open marine pelagic ecosystems, shifts in the physical environment can displace species over large spatial scales, which can further obscure the importance of trophic links within the system. El Niño events are typically associated with a shift in more southerly species of zooplankton (Keister et al. 2005) and

predatory nekton species (Pearcy 2002). Many nekton species are highly migratory and can expand and contract their distributions with varying ocean conditions (Brodeur et al. 2005).

Our perception of the NCC food web are therefore influenced by the scale we choose to use (Martinez 1993). It is apparent from previous studies that this system is open to extrinsic factors and external subsidies from other systems, and that these processes are inherently intertwined. Extrinsic factors of atmospheric teleconnections can control seasonal coastal upwelling and the relative strength of the California Current, which in turn influences trophic subsidies by influencing nutrient and organism movement into and out of the system. The difficulty in applying general concepts to this system (as well as other systems) is due to a myriad of factors, which directly and indirectly control ecosystem persistence through space and time (Wootton 1994). It is therefore important to understand the system as a sub-component of a larger system. Additional research is warranted to link the NCC to the rest of the California Current and the larger Pacific Ocean basin (McFarlane and McKinnell 2005).

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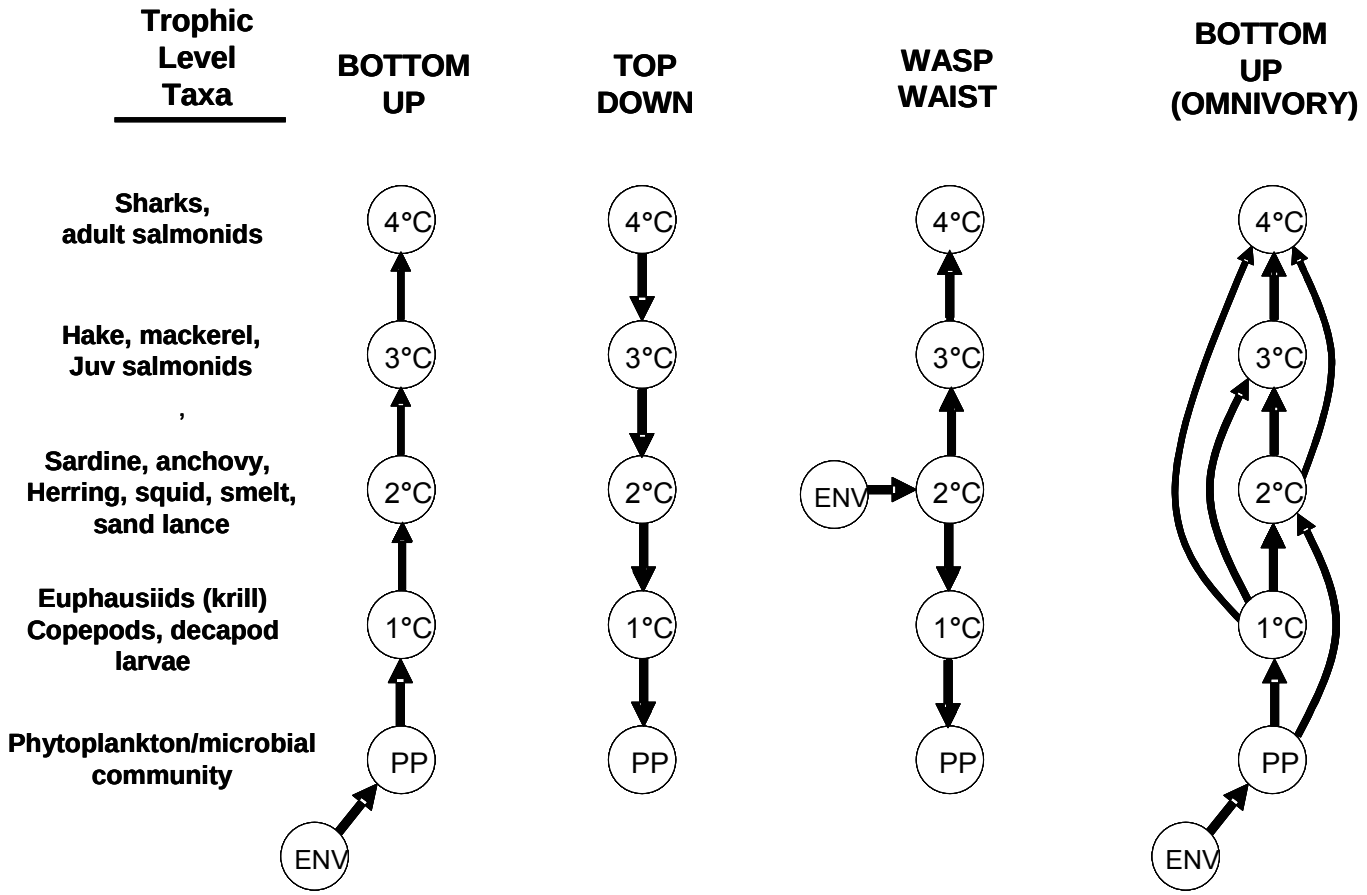

Figure 6.1. General diagrams of different control mechanisms of ecosystems. Arrows denote direction of control. Abbreviations within trophic nodes are denoted as the following: Environmental/abiotic affects (ENV), primary production (PP), primary-tertiary consumers (1°C to 4°C).Bottom-up control with omnivory (far right) is more indicative of the Northern California Current pelagic ecosystem during the time of this study (year 2000 and 2002).

APPENDIX

APPENDIX. Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

Nekton Species
Surf smelt (*Hypomesus pretiosus*)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Appendicularia	<0.1 (<0.1)	<0.1 (1.0)		<0.1 (1.8)
Polychaeta	<0.1 (<0.1)		0.1 (<0.1)	1.4 (2.6)
Mollusca				
Gastropoda			<0.1 (<0.1)	0.5 (13.4)
Pteropoda				1.5 (8.2)
Insecta				
Diptera	<0.1 (<0.1)	0.1 (0.1)		
Arachnida	<0.1 (<0.1)			
Chaetognatha	0.6 (0.2)		1.5 (0.4)	
Cnidaria (polyp larva)	20.6 (2.7)	8.8 (0.3)	26.5 (0.4)	
Ctenophora (unidentified)	<0.1 (<0.1)			
Crustacea (unidentified)		0.1 (0.1)	<0.1 (0.1)	<0.1 (0.1)
Cladocera				
Podon sp.		<0.1 (0.2)		<0.1 (0.3)
Cirripedia (cyprid)		0.1 (1.1)	<0.1 (<0.1)	<0.1 (1.3)
(nauplii)				<0.1 (0.3)
Cumacea			<0.1 (<0.1)	
Mysida		1.6 (0.3)	0.9 (<0.1)	
Neomysis kadiakensis	0.1 (<0.1)			
Copepoda (egg)		<0.1 (0.1)		
(copepedite)	0.8 (7.0)	<0.1 (0.2)		
(adult)	0.3 (1.3)	3.8 (57.1)	6.8 (89.4)	0.1 (6.9)
Acartia sp.		<0.1 (0.8)		
Calanus marshallae	0.5 (1.4)	0.4 (0.4)		
Calanus sp.	0.4 (1.2)	0.3 (0.8)	4.1 (4.3)	
Centropages sp.		0.9 (9.8)		
Epilabidocera amphitrites		<0.1 (0.1)		
Epilabidocera sp.			<0.1 (<0.1)	
Eucalanus sp.	0.1 (0.2)	0.7 (0.9)	1.4 (0.7)	0.1 (1.8)
Pseudocalanus sp.	6.3 (<0.1)	<0.1 (0.4)		
Material	<0.1 ( )			
Amphipoda	<0.1 (<0.1)	0.5 (0.2)		
Gammaridea				
Atylus tridens		0.2 (0.1)	0.2 (<0.1)	
Jassa sp.	<0.1 (<0.1)	0.1 (0.1)		

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Hyperiidea	1.2 (0.6)	5.6 (1.7)	0.6 (0.2)	1.2 (4.9)
Hyperia medusarum	0.1 (<0.1)	6.5 (1.7)	0.6 (<0.1)	<0.1 (0.3)
Hyperoche medusarum	0.5 (0.2)	3.3 (1.1)	26.7 (0.6)	0.6 (4.1)
Primno brevidens		0.2 (0.1)		0.8 (1.5)
Themisto pacifica	0.3 (0.1)	2.7 (1.2)	<0.1 (<0.1)	1.2 (2.1)
Vibilia australis	13.5 (16.5)			
Vibilia sp.	<0.1 (<0.1)			
Vibilia wolterecki	<0.1 (<0.1)			
Material	5.3 ( )	32.4 ( )	5.1 ( )	1.8 ( )
Decapoda (larva)	0.7 (0.4)	7.6 (12.7)	<0.1 (<0.1)	<0.1 (0.3)
(zoea)	<0.1 (<0.1)	0.1 (0.3)	0.1 (0.1)	1.2 (2.1)
(meg.)		0.9 (1.6)		
Brachyura (larva)		0.5 (0.3)		
(zoea)	<0.1 (0.1)		<0.1 (<0.1)	<0.1 (0.5)
(meg.)	0.7 (0.2)	0.2 (0.2)	3.1 (0.5)	
Cancer magister (meg.)			0.1 (<0.1)	
C. antennarius/gracilis (meg.)			0.2 (<0.1)	
C. oregonensis/productus (meg.)	0.2 (0.1)		3.6 (0.5)	0.8 (1.3)
Cancer sp. (zoea)	1.5 (0.6)	1.1 (0.3)		
(meg.)	23.1 (2.8)		<0.1 (<0.1)	
Pachycheles pubescens				
(zoea)	<0.1 (<0.1)			
(meg.)	<0.1 (<0.1)	0.3 (0.1)		
Petrolisthes eriomerus				
(zoea)	<0.1 (<0.1)		0.1 (<0.1)	
(meg.)	<0.1 (<0.1)			
Petrolisthes sp. (meg.)			0.1 (0.1)	
Pinnotheridae (zoea)	<0.1 (<0.1)			
Pinnixa sp. (meg.)			0.8 (0.1)	
Fabia subquadrata (zoea)	0.1 (0.1)		0.1 (<0.1)	
(meg.)	<0.1 (<0.1)		5.1 (0.7)	
Material			0.8 ( )	
Porcellanidae (larva)			0.2 (<0.1)	
(zoea)	<0.1 (<0.1)	<0.1 (0.1)		
(meg.)		<0.1 (0.1)	0.5 (0.4)	
Paguridae				
Pagurus ochotensis (meg.)		2.2 (0.6)		
Pagurus sp. (zoea)		<0.1 (0.1)	0.1 (<0.1)	
(meg.)		1.0 (0.3)	0.3 (0.1)	

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Callianassidae				
Neotrypaea californiensis				
(zoea)			0.3 (0.3)	
Caridea (zoea)	<0.1 (<0.1)			
(meg.)	0.2 (<0.1)	0.5 (0.6)		
(juv.)	0.2 (<0.1)	<0.1 (0.2)		
Crangonidae (larva)		0.5 (0.1)		
(zoea)	0.2 (0.4)		0.3 (<0.1)	
(meg.)		0.5 (0.2)	0.1 (<0.1)	
(juv.)			<0.1 (<0.1)	
Hippolytidae (zoea)			0.1 (<0.1)	
(meg.)			<0.1 (<0.1)	
(juv.)		0.1 (0.1)	<0.1 (<0.1)	
Pandalidae (juv.)		0.1 (0.1)	0.2 (<0.1)	
Pandalus sp. (meg.)			0.1 (<0.1)	
Anomura (larva)		0.2 (0.1)	0.4 (0.1)	
(meg.)	0.1 (<0.1)		0.1 (<0.1)	
Euphausiacea (egg)	0.5 (62.1)			
(calytopis)		<0.1 (0.1)		
(furcilia)		0.5 (1.5)		<0.1 (0.3)
(adult)	1.8 (0.1)			2.4 (1.0)
Euphausia pacifica (adult)	0.3 (<0.1)			
Thysanoessa spinifera				
(furcilia)				3.3 (20.1)
(adult)	0.6 (<0.1)			13.2 (3.6)
Material	0.4 ( )			1.4 (0.3)
Gelatinous Material	0.9 (<0.1)			25.9 (8.5)
Salpa/*Thetys*	<0.1 (<0.1)			
Siphonophorae	0.3 (<0.1)			
Unidentified invertebrate (egg)	<0.1 (<0.1)	<0.1 (0.2)	<0.1 (<0.1)	
Osteichthyes (egg)	1.1 (1.2)	<0.1 (0.1)	<0.1 (0.1)	<0.1 (0.3)
(larva)	0.8 (<0.1)		0.5 (<0.1)	0.7 (0.5)
(juv.)	1.9 (<0.1)	1.8 (0.1)		
Flatfish (larva)	<0.1 (<0.1)		0.2 (<0.1)	
Osmeridae (larva)	0.1 (<0.1)			
Material	0.4 (<0.1)			
Plant matter	<0.1 ( )			
Unidentified material	13.2 ( )	12.2 ( )	7.6 (0.1)	41.8 (11.1)

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APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

Nekton Species **Sablefish (*Anoplopoma fimbria*)**				
	Percent wet weight (Percent N)			
	2000		**2002**	
Prey Taxa	**June**	**August**	**June**	**August**
Crustacea				1.9 (0.9)
Amphipoda				
Hyperiidea				0.1 (0.9)
Hyperoche medusarum	4.0 (16.7)			0.3 (3.0)
Themisto pacifica		<0.1 (1.0)		<0.1 (0.4)
Decapoda (larva)				<0.1 (0.4)
Brachyura				
Cancer sp. *(meg.)*				0.4 (2.1)
C. magister (meg.)		26.6 (57.1)		7.7 (16.6)
C. oregonensis/productus (meg.)				0.9 (6.0)
Euphausiacea (adult)	96.0 (83.3)	3.9 (2.9)		28.7 (31.1)
Euphausia pacifica (adult)		5.6 (6.7)		
Thysanoessa spinifera (adult)		33.7 (30.5)		47.7 (33.2)
Osteichthyes (larva)				1.4 (0.9)
(juv.)		15.6 (1.9)		
Flatfish (larva)				1.9 (0.4)
Material		12.0 ( )		3.0 (1.3)
Unidentified material		2.5 ( )		6.0 (3.0)
Nekton Species **Spiny Dogfish (*Squalus acanthias*)**				
Cnidaria				
Siphonophora			0.6 (3.1)	
Nanomia bijuga			11.1 (15.6)	
Polychaeta			<0.1 (3.1)	
Crustacea				
Copepoda			<0.1 (6.3)	
Amphipoda				
Hyperiidea			0.1 (9.4)	
Hyperia medusarum			<0.1 (3.1)	
Decapoda (zoea)			<0.1 (3.1)	
Euphausiacea (adult)			0.6 (9.4)	
Euphausia pacifica (adult)			0.3 (3.1)	
Thysanoessa spinifera (adult)			2.3 (12.5)	

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APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Material			2.0 ( )	
Gelatinous material			0.9 (3.1)	
Unidentified material			82.1 (28.1)	
Nekton species				
Bank rockfish (*Sebastes rufus*)				
Crustacea				
Copepoda (copepodite)			1.3 (66.7)	
(adult)			1.3 (33.3)	
Material			5.4 ( )	
Unidentified material			92.0 ( )	
Nekton species				
Canary rockfish (*Sebastes pinniger*)				
Chaetognatha			2.9 (0.8)	
Crustacea				
Copepoda			9.2 (24.1)	
Pseudocalanus sp. (adult)			0.5 (1.2)	
Euphausiacea (furcilia)			65.2 (73.5)	
Material			15.7 ( )	
Unidentified material			6.5 (0.4)	
Nekton Species				
Darkblotched rockfish (*Sebastes crameri*)				
Chaetognatha			<0.1 (0.2)	
Crustacea				
Cirripedia (cyprid larva)	1.4 (41.2)		<0.1 (0.2)	
Copepoda	<0.1 (1.0)		2.6 (42.5)	
Calanus sp.			0.4 (0.5)	
C. marshallae	25.7 (55.9)			
Pseudocalanus sp.			0.2 (3.6)	
Amphipoda				
Hyperiidea			0.4 (0.8)	
Vibilia australis			28.8 (17.6)	
Decapoda (larva)			0.1 (0.4)	
Brachyura				
Cancer sp. (meg.)			2.3 (0.2)	

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APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Euphausiacea (egg)	20.0 (2.0)		0.5 (33.9)	
(adult)	52.9 ( )			
Material			16.9 (0.2)	
Gelatinous Material			46.6 (0.2)	
Unidentified material			1.0 ( )	
Nekton Species				
Widow rockfish (*Sebastes entomelas*)				
Appendicularia			0.1 (0.1)	
Chaetognatha			0.1 (<0.1)	
Crustacea (larva)			0.2 (<0.1)	
Copepoda			52.5 (54.6)	
Calanus sp.			1.1 (0.1)	
Eucalanus sp.			0.2 (0.1)	
Epilabidocera sp.			0.2 (<0.1)	
Epilabidocera amphitrites			0.4 (0.1)	
Pseudocalanus sp.			0.1 (0.1)	
Material			0.9 ( )	
Amphipoda				
Hyperiidea				
Hyperia medusarum			<0.1 (<0.1)	
Themisto pacifica			0.2 (<0.1)	
Decapoda (larva)			0.2 (<0.1)	
(zoea)			<0.1 (<0.1)	
Euphausiacea (egg)			5.7 (40.4)	
(calytopis)			2.1 (2.1)	
(furcilia)			11.6 (2.4)	
(adult)			1.6 (<0.1)	
Euphausia pacifica (furcilia)			0.3 (<0.1)	
Thysanoessa spinifera (furcilia)			1.0 (0.3)	
Material			0.6 ( )	
Material			4.2 ( )	
Osteichthyes (larva)			12.4 (0.1)	
Unidentified material			4.4 ( )	
Appendicularia	3.3 (1.9)			
Crustacea	0.1 (0.1)			
Copepoda (copepodite)	15.0 (41.4)			

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

Nekton Species **Yellowtail Rockfish (*Sebastes flavidus*)**				
	Percent wet weight (Percent N)			
	2000		**2002**	
Prey Taxa	**June**	**August**	**June**	**August**
(adult)	67.1 (55.3)			
Calanus sp. (adult)	0.8 (0.1)			
Amphipoda				
Hyperiidea	1.3 (0.5)			
Decapoda (larva)	0.1 (0.1)			
(meg.)	1.6 (0.1)			
Euphausiacea (egg)	0.2 (0.9)			
Material	8.0 ( )			
Unidentified material	3.0 ( )			
Nekton Species **Jack Mackerel (*Trachurus symmetricus*)**				
Cnidaria (polyp larva)		0.1 (0.1)		
Polychaeta			0.1 (0.1)	
Pteropoda		0.1 (0.1)		
Mollusca				
Bivalvia		0.1 (0.1)		
Gastropoda			0.1 (0.1)	
Olivalle sp.		0.2 (0.2)		
Cephalopoda		0.1 (0.1)	3.2 (0.6)	0.2 (0.1)
Loligo opalescens				
Crustacea				
Copepoda			0.1 (0.1)	
Amphipoda				
Hyperiidea		0.1 (0.1)	0.3 (0.3)	0.4 (0.5)
Hyperia medusarum		0.2 (0.2)	0.3 (0.2)	0.1 (0.2)
Hyperoche medusarum		0.1 (0.1)	0.3 (0.9)	
Themisto pacifica			0.1 (0.1)	
Vibilia sp.			0.1 (0.1)	
V. australis			0.2 (2.2)	
V. cultripes			0.1 (0.1)	
Decapoda				
Brachyura (meg.)			0.1 (0.1)	
Cancer sp. (zoea)		0.1 (0.1)		
(meg.)		0.1 (0.1)	0.1 (0.1)	0.1 (0.2)
C. magister (meg.)		0.6 (1.3)	12.5 (10.4)	0.3 (0.9)

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
C. antennarius/gracilis (meg.)			0.1 (0.1)	0.1 (0.3)
C. oregonensis/productus (meg.)		0.1 (0.1)	0.4 (1.3)	0.2 (1.3)
Fabia subquadrata (zoea)			0.1 (0.1)	
(meg.)			0.1 (0.2)	
Pandalidae				
Pandalus danae (zoea)			0.1 (0.1)	
Sergestidae				
Sergestes similis			4.1 (3.0)	
Euphausiacea (egg)			0.1 (62.4)	
(adult)	13.8 (29.1)	7.9 (12.0)	9.1 (5.2)	16.6 (47.3)
Euphausia pacifica (adult)	37.3 (68.6)	56.4 (79.8)	13.5 (11.4)	12.1 (24.0)
Thysanoessa spinifera (adult)	1.3 (1.7)	6.8 (6.5)	0.7 (0.9)	6.1 (23.8)
Material	41.7 ( )	21.0 ( )	1.2 ( )	9.8 ( )
Material		6.6 ( )	23.4 ( )	48.7 ( )
Osteichthyes (egg)			0.1 (0.1)	
(larva)			3.3 (0.4)	1.0 (0.7)
(juv.)		0.1 (0.1)	1.7 (0.3)	0.3 (0.3)
Ammodytidae				
Ammodytes hexapterus (juv.)	6.1 (0.7)	0.6 (0.1)	5.8 (0.6)	
Clupeidae (larva)				0.2 (0.1)
Cottidae (larva)				0.1 (0.1)
(juv.)		0.1 (0.1)	0.1 (0.1)	
Hemilepidotus sp. (larva)			0.4 (0.1)	
(juv.)			0.7 (0.1)	
Flatfish (larva)		0.2 (0.1)	1.8 (0.2)	0.4 (0.2)
Glyptocephalus zachirus (larva)				0.7 (0.4)
Microstomus pacificus (larva)				0.7 (0.2)
Pleuronichthys coenosus (larva)				0.1 (0.1)
Hexagrammidae				
Hexagrammos decagrammus (juv.)				0.1 (0.1)
Osmeridae (larva)				0.4 (0.3)
Scorpaenidae				
Sebastes sp. (larva)			0.2 (0.1)	0.4 (0.4)
(juv.)		0.1 (0.1)	4.2 (0.2)	0.1 (0.1)

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Material		0.2 ( )	1.4 ( )	0.6 ( )
Gelatinous material		0.1 ( )	3.8 ( )	
Plant material (seed)				0.1 (0.1)
Unidentified material		0.3 ( )	8.9 ( )	2.2 ( )
Nekton Species				
Blue Shark (*Prionace glauca*)				
Mollusca				
Cephalopoda		0.9 (0.1)	1.1 (60.0)	0.7 (50.0)
Loligo opalescens				6.1 (16.7)
Crustacea				
Euphausiacea (adult)		15.5 (94.1)		
Euphausia pacifica (adult)		5.0 (5.6)		
Material		4.4 ( )		
Osteichthyes				
Merlucciidae				
Merluccius productus (adut)			30.6 (10.0)	
Carangidae				
Trachurus symmetricus (adult)			57.2 (10.0)	
Clupeidae (adult)		50.7 (0.1)	1.1 (10.0)	27.1 (33.3)
Sardinops sagax (adult)			9.2 (10.0)	
Material		3.9 ( )	0.7 ( )	66.1 ( )
Unidentified material		19.8 ( )		
Nekton Species				
Market squid (*Loligo opalescens*)				
Chaetognatha			0.1 (0.9)	
Mollusca				
Cephalopoda				
Loligo opalescens			<0.1 (0.1)	0.3 (66.7)
Crustacea				
Copepoda	<0.1 (5.3)			
Decapoda (larva)	1.8 (0.8)		10.3 (7.7)	
(meg.)			0.5 (0.6)	
(adult)			0.5 (1.1)	
Brachyura (larva)	10.3 (3.1)		0.1 (0.6)	
Cancer sp. (meg.)	21.2 (1.5)		0.1 (0.3)	
Pinnotheridae (zoea)			31.8 (87.2)	

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Material			17.2 ( )	
Euphausiacea (egg)	1.8 (87.0)			
Thysanoessa spinifera (adult)	31.0 (0.8)		0.3 (0.1)	
Material				1.0 ( )
Material	6.1 ( )		31.8 ( )	51.5 ( )
Gelatinous Material				9.3 ( )
Insecta (material)			<0.1 ( )	
Osteichthyes (larva)	27.8 (1.5)		3.2 (1.0)	3.6 (33.3)
Material			0.6 (0.3)	13.6 ( )
Unidentified material			3.4 ( )	20.6 ( )
Nekton Species				
Lingcod, juvenile (*Ophiodon elongates*)				
Crustacea				
Copepoda				
Calanus sp. (adult)	33.4 (57.8)		67.8 (97.6)	
Euphausiacea (furcilia)	38.4 (28.2)			
Thysanoessa spinifera (furcilia)	23.5 (13.4)			
(adult)	4.0 (0.6)			
Material	0.7 ( )		2.2 ( )	
Osteichthyes (larva)			30.0 (2.4)	
Nekton Species				
Whitebait smelt (*Allosmerus elongates*)				
Polychaeta				33.2 (8.3)
Pteropoda		<0.1 (0.1)		
Crustacea				
Ostracoda		<0.1 (<0.1)		
Cladocera				
Evadne sp.		<0.1 (<0.1)		
Cirripedia (cyprid larva)	<0.1 (1.1)			
Mysida		1.0 (0.1)		
Cumacea				
Diastylopsis dawsoni			13.8 (27.9)	
Amphipoda				
Caprellidea		0.1 (<0.1)		
Gammaridea				<0.1 (1.4)

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Atylus tridens		0.7 (0.1)		
Hyperiidea		0.2 (0.1)		0.2 (1.4)
Hyperia medusarum		<0.1 (<0.1)		1.9 (1.4)
Hyperoche medusarum		1.0 (0.2)		0.2 (1.4)
Themisto pacifica		0.3 (0.4)		
Vibilia australis	<0.1 (0.1)			
Material	<0.1 ( )			
Copepoda (copepidite)	<0.1 (0.6)	<0.1 (<0.1)		
(adult)	0.5 (3.9)	<0.1 (<0.1)	0.6 (5.2)	2.4 (52.7)
Calanus sp.		<0.1 (0.1)		0.3 (4.2)
C. marshallae		<0.1 (<0.1)		
Epilabidocera sp.		<0.1 (<0.1)		
Decapoda (larva)	0.2 (3.0)	0.3 (0.1)	1.0 (2.0)	1.1 (5.6)
Brachyura (larva)		0.1 (0.1)		
Cancer sp. (meg.)		0.7 (0.3)		
(zoea)	<0.1 (0.1)			
C. antennarius/gracilis (meg.)				0.4 (1.4)
C. magister (meg.)			2.9 (3.1)	
C. oregonensis/productus (meg.)			4.2 (6.2)	0.7 (2.8)
Porcellanidae				
Pachycheles pubescens				
(meg.)		<0.1 (<0.1)		
(zoea)		<0.1 (<0.1)		
Petrolisthes sp. (zoea)			0.2 (2.1)	
Pinnotheridae (zoea)		0.1 (0.1)		
(meg.)		<0.1 (<0.1)		
Fabia subquadrata (zoea)		0.1 (0.1)	5.7 (10.3)	
(meg.)			7.9 (14.4)	
Pinnixa sp. (meg.)		0.1 (0.1)		
Paguridae (zoea)		1.2 (0.7)		
(meg.)		0.6 (0.3)		
Pagurus sp. (zoea)		1.1 (0.5)		
(meg.)		0.6 (0.3)		
P. ochotensis (zoea)		0.3 (0.2)		
(meg.)		1.0 (0.3)		
Orthopagurus schmitti (meg.)		0.1 (<0.1)		
Discorsopagurus schmitti (meg.)		0.2 (0.1)		

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Caridea (larva)		0.1 (0.1)	2.5 (1.0)	
(zoea)	<0.1 (0.1)			
(meg.)		0.1 (<0.1)		
(juv.)		1.3 (0.4)		
Crangonidae (zoea)		30.0 (40.3)		
(meg.)		6.8 (1.5)	1.9 (1.0)	
(juv.)		0.6 (0.1)		
Pandalidae				
Pandalus danae (meg.)			1.3 (1.0)	
P. jordani (juv.)		0.4 (0.2)	1.8 (1.0)	
Euphausiacea (egg)	33.4 (3.0)	3.7 (0.1)	6.9 (5.2)	12.4 (5.6)
(furcilia)	0.3 (76.8)			
(adult)		0.3 (0.6)		
Euphausia pacifica (adult)	12.2 (0.9)			
Thysanoessa spinifera				
(furcilia)		30.6 (48.8)		
(adult)	51.3 (3.0)	6.3 (0.1)	18.7 (6.2)	46.7 (12.5)
Osteichthyes (larva)		1.2 (0.1)	12.6 (1.0)	
(juv.)		2.1 (0.3)		
Cottidae (larva)		0.8 (0.1)		
(juv.)		0.8 (<0.1)		
Material	2.0 (7.4)	1.6 ( )	15.8 (10.3)	0.3 (1.4)
Unidentified matter	0.1 ( )	0.2 ( )	2.1 (2.1)	
Nekton Species				
Pacific Saury (*Cololabis saira*)				
Chaetognatha		0.1 (1.0)		0.1 (<0.1)
Polychaeta				<0.1 (<0.1)
Pteropoda			2.1 ( )	
Mollusca				
Gastropoda				<0.1 (<0.1)
Crustacea				
Cirripedia (nauplii)				<0.1 (<0.1)
(cyprid)		<0.1 (1.0)		<0.1 (<0.1)
Copepoda		0.3 (36.1)		9.4 (0.6)
Calanus sp.		<0.1 (1.6)		0.4 (0.1)

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Amphipoda				
Hyperiidea		<0.1 (0.5)	<0.1 (0.3)	0.2 (<0.1)
Hyperia medusarum				0.2 (<0.1)
Primno brevidens				<0.1 (<0.1)
Decapoda				
Brachyura				
Cancer magister (meg.)			6.5 (9.0)	
Euphausiacea (egg)				3.6 (99.0)
(adult)		14.8 (19.9)		0.3 (<0.1)
Euphausia pacifica (adult)		32.9 (38.7)		
Thysanoessa spinifera (adult)				0.1 (<0.1)
Material		43.8 ( )		0.4 (<0.1)
Material		5.3 ( )	20.6 ( )	15.3 ( )
Osteichthyes (egg)		0.1 (0.5)	11.0 (82.0)	0.4 (<0.1)
(larva)			4.1 (0.8)	<0.1 (<0.1)
(juv.)		0.8 (0.5)	21.6 (3.1)	<0.1 (<0.1)
Ammodytidae				
Ammodytes hexapterus (juv.)			1.2 (0.3)	
Cottidae				
Hemilepidotus sp. (juv.)			13.2 (2.9)	
Material				5.8 ( )
Gelatinous Material				36.6 (0.1)
Invertebrate (egg)				<0.1 (0.1)
Unidentified material		1.9 ( )	18.7 ( )	29.6 ( )
Nekton Species				
Pacific Sardine (*Sardinops sagax*)				
Appendicularia	<0.1 (0.8)	0.2 (0.2)	2.7 (5.9)	
Chaetognatha		<0.1 (<0.1)	0.5 (0.1)	
Pteropoda		0.4 (<0.1)		
Crustacea				
Amphipoda	<0.1 (0.8)			
Hyperiidea		0.3 (0.1)	0.1 (0.1)	<0.1 (<0.1)
Vibilia australis	0.2 (1.5)		0.9 (2.1)	0.3 (0.7)
Cirripedia (nauplii)			<0.1 (0.9)	<0.1 (0.1)
(cyprid)			<0.1 (0.1)	
Cladocera				<0.1 (<0.1)
Copepoda (egg)		<0.1 (1.1)	<0.1 (0.1)	<0.1 (0.2)
(nauplii)		<0.1 (7.3)		

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
(copepedite)		0.1 (19.6)		<0.1 (<0.1)
(adult)	<0.1 (0.8)	0.2 (19.1)	57.5 (42.5)	0.6 (27.7)
Acartia sp.		0.8 (11.0)	<0.1 (0.3)	
Calanus sp.		0.1 (0.4)	0.7 (2.8)	<0.1 (0.6)
Centropages sp.		<0.1 (0.6)		
Oithona sp.		<0.1 (0.5)		
Pseudocalanus sp.		0.7 (8.8)	0.3 (13.4)	<0.1 (0.2)
Decapoda				
Brachyura (zoea)	<0.1 (0.4)		<0.1 (<0.1)	
(meg.)			<0.1 (0.1)	
Cancer sp. (meg.)		<0.1 (<0.1)		
Fabia subquadrata (zoea)			<0.1 (<0.1)	<0.1 (<0.1)
(meg.)			<0.1 (<0.1)	
Caridea (larva)		<0.1 (<0.1)		
Euphausiacea (egg)	0.1 (87.3)	0.3 (29.3)	3.0 (15.3)	0.2 (54.0)
(nauplii)		<0.1 (0.9)	<0.1 (1.3)	<0.1 (11.0)
(calytopis)		<0.1 (0.4)	<0.1 (0.2)	<0.1 (<0.1)
(furcilia)		0.1 (0.2)	0.1 (1.2)	
(adult)			0.1 (0.1)	3.5 (1.1)
Euphausia pacifica (adult)	10.0 (6.9)	74.7 (1.1)	0.9 (0.1)	1.3 (0.2)
Thysanoessa spinifera (furcilia)			<0.1 (<0.1)	
(adult)	2.6 (0.8)		0.3 (<0.1)	16.4 (4.0)
Material	23.1 ( )	0.2 ( )		0.2 ( )
Material	34.8 ( )		0.1 ( )	0.6 ( )
Gelatinous Material	2.3 ( )		0.1 ( )	0.2 ( )
Insecta				<0.1 (<0.1)
Unidentified invertebrate (egg)		<0.1 (<0.1)	<0.1 (12.8)	
Osteichthyes (egg)	<0.1 (0.8)	0.4 (<0.1)	<0.1 (<0.1)	<0.1 (0.2)
(larva)			0.3 (<0.1)	
(juv.)		<0.1 (<0.1)		
Fish Scale			0.3 (0.2)	<0.1 (<0.1)
Phytoplankton	3.8 ( )	6.0 ( )	28.0 ( )	74.8 ( )
Unidentified material	23.0 ( )	15.8 ( )	3.7 (0.1)	1.8 ( )

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

Nekton Species
Pacific Sand lance (*Ammodytes hexapterus*)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Chaetognatha			0.1 (<0.1)	
Pteropoda			<0.1 (<0.1)	
Crustacea				
Amphipoda				
Gammaridea			<0.1 (<0.1)	
Hyperiidea			2.4 (0.6)	
Hyperoche medusarum			0.1 (<0.1)	
Lycaea pulex			1.7 (0.4)	
Themisto pacifica			<0.1 (<0.1)	
Vibilia australis			35.7 (21.0)	
V. wolterecki			<0.1 (<0.1)	
Copepoda (copepedite)			8.3 (20.6)	
(adult)			0.5 (5.5)	
Calanus sp.			<0.1 (0.1)	
C. marshallae			1.0 (0.9)	
Material			13.1 ( )	
Decapoda (zoea)			<0.1 (0.1)	
(larva)			<0.1 (<0.1)	
(juv.)			<0.1 (<0.1)	
Brachyura (zoea)			<0.1 (<0.1)	
(meg.)			0.1 (<0.1)	
Cancer sp. (zoea)			<0.1 (<0.1)	
C. oregonensis/productus (meg.)			5.7 (0.6)	
Pinnotheridae				
Fabia subquadrata (zoea)			<0.1 (<0.1)	
(meg.)			<0.1 (0.1)	
Paguridae				
Pagurus sp. (zoea)			0.1 (<0.1)	
(meg.)			<0.1 (<0.1)	
Porcellanidae (zoea)			0.4 (0.3)	
(meg.)			<0.1 (<0.1)	
Pachycheles sp. (zoea)			0.1 (0.1)	
P. eriomerus (meg.)			0.1 (<0.1)	
Petrolisthes sp. (zoea)			<0.1 (<0.1)	

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Caridea (zoea)			0.4 (0.1)	
(meg.)			1.0 (0.2)	
(juv.)			<0.1 (<0.1)	
Euphausiacea (egg)			0.7 (48.8)	
Thysanoessa spinifera (adult)			24.6 (0.3)	
Gelatinous Material			0.1 ( )	
Osteichthyes (egg)			<0.1 (0.1)	
(larva)			1.0 (<0.1)	
Unidentified material			2.7 ( )	
Nekton Species				
Pacific Mackerel (*Scomber japonicus*)				
Prey Taxa	**June**	**August**	**June**	**August**
Mollusca				
Cephalopoda				
Loligo opalescens		16.0 (2.3)		
Pteropoda		<0.1 (2.3)		
Crustacea				
Decapoda				
Brachyura				
Cancer magister (meg.)		0.2 (2.3)		
Euphausiacea (adult)		36.1 (88.4)		
Material		38.9 ( )		
Material		1.6 ( )		
Osteichthyes (juv.)		3.6 (2.3)		
Material		0.1 (2.3)		
Unidentified material		3.5 ( )		
Nekton Species				
Pacific Herring (*Clupea pallasi*)				
Appendicularia			1.0 (25.4)	
Chaetognatha			0.2 (0.1)	<0.1 (<0.1)
Polychaeta			0.9 (<0.1)	
Pteropoda	<0.1 (<0.1)			0.4 (3.0)
Mollusca				
Gastropoda				<0.1 (0.6)
Cephalopoda				
Loligo opalescens			0.7 (<0.1)	
Crustacea				

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Cirripedia (nauplii)	<0.1 (3.0)			
(cyprid)	<0.1 (<0.1)		<0.1 (0.9)	<0.1 (<0.1)
Lepas sp. (cyprid)				<0.1 (<0.1)
Mysida	<0.1 (<0.1)		0.1 (<0.1)	<0.1 (<0.1)
Neomysis kadiakensis				0.1 (<0.1)
Amphipoda	<0.1 (<0.1)			
Gammaridea	<0.1 (<0.1)			<0.1 (<0.1)
Atylus tridens				<0.1 (0.1)
Hyperiidea	<0.1 (0.1)		<0.1 (<0.1)	0.3 (0.5)
Hyperia medusarum				2.9 (<0.1)
Hyperoche martinezi	<0.1 (<0.1)			
H. medusarum	<0.1 (<0.1)		<0.1 (<0.1)	0.3 (0.5)
Lycaea pulex	0.5 (0.7)			
Themisto pacifica	0.2 (0.2)		0.1 (0.1)	1.9 (2.1)
Vibilia australis	7.5 (26.1)			
Material	1.0 ( )			<0.1 ( )
Copepoda (copepedite)	0.4 (30.1)			
(adult)	0.2 (1.8)		1.9 (26.1)	0.2 (6.0)
Calanus sp.	0.2 (2.0)		7.5 (21.8)	1.7 (14.4)
C. marshallae	0.7 (8.6)			
Epilabidocera sp.				<0.1 (<0.1)
Eucalanus sp.			0.1 (0.1)	<0.1 (<0.1)
Pseudocalanus sp.	<0.1 (<0.1)			<0.1 (<0.1)
Material	5.9 ( )		26.6 ( )	4.4 ( )
Decapoda (larva)	0.3 (4.0)		1.2 (0.7)	<0.1 (0.1)
(zoea)	0.1 (0.5)		0.4 (0.4)	0.1 (0.3)
(meg.)	<0.1 (<0.1)		0.1 (0.1)	
Anomura (meg.)			0.1 (0.1)	
Brachyura (larva)	<0.1 (<0.1)			
(zoea)	<0.1 (0.2)		<0.1 (<0.1)	
(meg.)	<0.1 (0.1)		<0.1 (<0.1)	<0.1 (<0.1)
Cancer sp. (zoea)	<0.1 (<0.1)		<0.1 (<0.1)	
(meg.)	0.1 (<0.1)		1.4 (0.6)	
C. antennarius/gracilis (meg.)			0.3 (0.1)	<0.1 (<0.1)
C. magister (meg.)			0.1 (<0.1)	
C. oregonensis/productus (meg.)	0.7 (0.4)		0.3 (0.1)	0.1 (<0.1)
Paguridae				

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Pagurus sp. (zoea)	<0.1 (<0.1)		0.4 (0.4)	0.3 (3.0)
(meg.)	<0.1 (<0.1)		<0.1 (<0.1)	
Pinnotheridae (zoea)	<0.1 (<0.1)		<0.1 (<0.1)	
Fabia subquadrata (zoea)	<0.1 (0.1)		0.1 (0.1)	
(meg.)			7.5 (2.3)	<0.1 (<0.1)
Porcellanidae (larva)	<0.1 (<0.1)			
(zoea)	<0.1 (0.3)			
Pachycheles pubescens (larva)	0.1 (0.1)			
Petrolisthes eriomerus (meg.)	<0.1 (<0.1)			
Callianassidae *Neotrypaea californiensis* (zoea)	<0.1 (<0.1)			
Caridea (zoea)	<0.1 (0.1)			
(meg.)	<0.1 (0.1)			
(juv.)	<0.1 (<0.1)		<0.1 (<0.1)	<0.1 (<0.1)
Crangonidae (zoea)	0.7 (4.6)			
(meg.)			0.2 (0.1)	
(juv.)				<0.1 (<0.1)
Crangon sp. (zoea)				<0.1 (<0.1)
(meg.)			0.9 (0.1)	<0.1 (<0.1)
Pandalidae (zoea)	<0.1 (<0.1)			
(meg.)	<0.1 (<0.1)		0.3 (0.2)	
(juv.)	0.1 (0.1)			
Euphausiacea (egg)	<0.1 (10.2)		<0.1 (0.4)	0.1 (53.1)
(furcilia)	0.1 (0.2)		8.5 (12.8)	0.3 (1.0)
(adult)	17.3 (2.1)		2.8 (1.0)	20.3 (5.3)
Euphausia pacifica (adult)	3.1 (0.5)		0.4 (0.1)	10.2 (3.8)
Thysanoessa spinifera (furcilia)			2.1 (3.9)	<0.1 (<0.1)
(adult)	49.6 (3.2)		15.3 (0.7)	48.2 (5.6)
Material	6.7 ( )		4.2 (<0.1)	4.6 ( )
Unidentified invertebrate (egg)			<0.1 (<0.1)	
Osteichthyes (egg)	<0.1 (<0.1)		<0.1 (<0.1)	<0.1 (<0.1)
(larva)	0.4 (0.1)		0.2 (<0.1)	1.8 (0.2)
(juv.)	1.7 (0.1)		2.9 (0.1)	0.5 (0.1)
Ammodytidae *Ammodytes hexapterus* (juv.)				0.1 (<0.1)
Clupeidae (juv.)				0.1 (<0.1)

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Cottidae (juv.)			1.6 (0.2)	0.1 (<0.1)
Leptocottus armatus (juv.)			1.2 (0.1)	
Fish Scale			0.9 (0.4)	<0.1 (<0.1)
Material	0.4 ( )		<0.1 ( )	<0.1( )
Plant material (seed, wood)	<0.1 (<0.1)			<0.1 (<0.1)
Gelatinous Material			0.1 ( )	
Unidentified material	1.6 ( )		7.2 ( )	0.6 ( )
Nekton Species				
Pacific Hake (*Merluccius productus*)				
Crustacea			<0.1 (0.4)	
Decapoda				
Brachyura				
Cancer magister (meg.)			0.2 (1.6)	0.3 (0.5)
C. oregonensis/productus (meg.)			0.1 (2.7)	0.2 (0.6)
Fabia subquadrata (meg.)			0.6 (12.3)	
Euphausiacea (adult)			3.1 (35.3)	31.5 (55.7)
Euphausia pacifica (adult)			0.6 (3.3)	4.4 (5.0)
Thysanoessa spinifera (furcilia)			0.1 (2.7)	
(adult)			6.4 (39.5)	21.1 (37.8)
Material			0.8 ( )	11.9 ( )
Gelatinous material				
Osteichthyes (larva)				<0.1 (0.1)
(juvenile)			0.7 (0.7)	
Clupeidae				
Sardinops sagax (adult)			86.2 (0.2)	
Engraulidae				
Engraulis mordax (adult)				29.1 (0.1)
Fish Scale			0.1 (1.3)	0.1 (0.4)
Unidentified material			0.1 ( )	<0.1 ( )
Nekton Species				
Northern Anchovy (*Engraulis mordax*)				
Appendicularia (material)				0.6 ( )
Pteropoda				<0.1 (<0.1)
Mollusca				
Gastropoda			<0.1 (0.6)	
Crustacea			3.1 (11.7)	2.2 (0.9)

(CONTINUED)

APPENDIX (CONTINUED). Species-specific description of nekton diets (non-salmonid) as percent damp weight and percent total number. Description of detailed salmonid diets are given in Baldwin et al. in-prep.)

	Percent wet weight (Percent N)			
	2000		2002	
Prey Taxa	**June**	**August**	**June**	**August**
Cirripedia (cyprid)			<0.1 (1.2)	<0.1 (0.2)
Copepoda (egg)				<0.1 (0.8)
(adult)			6.7 (69.0)	0.1 (3.5)
Acartia sp.				<0.1 (<0.1)
Calanus sp.				<0.1 (0.1)
Pseudocalanus sp.				<0.1 (1.0)
Decapoda (larva)			<0.1 (0.6)	
(zoea)				<0.1 (<0.1)
Euphausiacea (egg)				0.2 (65.9)
(nauplii)				<0.1 (0.1)
(adult)				28.8 (11.4)
Euphausia pacifica (adult)				1.6 (0.4)
Thysanoessa spinifera (adult)		58.8 (100)		28.6 (11.1)
Material		41.2 ( )		6.8 ( )
Insecta			0.1 (0.6)	
Unidentified invertibrate (egg)				<0.1 (2.3)
Osteichthyes (egg)			0.8 (4.1)	<0.1 (0.2)
(larva)				0.2 (<0.1)
Material				0.2 (<0.1)
Phytoplankton			48.0 (10.0)	27.5 (1.7)
Plant matter (wood)			0.1 (1.8)	
Unidentified material			41.2 ( )	3.1 ( )