Zooplankton Data from High-Frequency Coastal Transects: Enriching the Contributions of Ocean Observing Systems to Ecosystem-Based Management in the Northern California Current[1]

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CHAPTER OUTLINE

[1]The opinions expressed herein are those of the authors and do not represent official policy of NOAA or the National Marine Fisheries Service.

1. INTRODUCTION

Collection of ocean data has grown tremendously in recent years, spurred in no small part by mandates to manage marine ecosystems holistically and the need to understand and forecast the consequences of anthropogenic climate change.[1,2] A broad suite of remote sensing technologies, whether satellite-borne or land-based, can be used to collect information on sea surface temperature, salinity, currents, winds, sea surface height, and ocean color (phytoplankton, CDOM, sediment) across broad swaths of the ocean. In situ sensors on moorings or at shore stations complement remote sensing by collecting high temporal resolution data near the coastline and throughout the water column—places where remote sensing instruments cannot see. Mobile observation platforms, whether ship-based or aboard autonomous underwater vehicles (AUVs), provide quasi-synoptic snapshots of a dynamic ocean.

In combination, existing data streams from these several approaches provide an increasingly rich view of the ocean's state and dynamics. Time series of physical observations are essential inputs for state-of-the-art data-assimilative models that, in turn, provide nowcasts of the current state of the ocean as well as short-term (e.g., 72-h) forecasts of ocean conditions.[3,4] Building on these successes, modelers are working to integrate remotely sensed biological proxies (e.g., chlorophyll concentration) into coupled biophysical models of the plankton ecosystem.[5] Such modeling efforts represent a significant step toward understanding how changes in physical forcing might impact ecosystems.

Notwithstanding the growing success and clear value of existing ocean observing system (OOS), physical observations and direct or proxy measures of nutrient or phytoplankton concentrations are one or more steps removed from higher trophic levels of marine ecosystems and species of more direct value to society. Even as ecosystem considerations become more prevalent in the management of living marine resources, there are few strong examples where observations at the base of the physics-to-fisheries system are rigorously and quantitatively integrated into managers' understanding of the dynamics of fisheries stocks or protected species.[6,7]

Data on zooplankton are essential for bridging this gap and, as we review below, can be supplied to resource managers in timely fashion by ship-based, sea-going elements of an OOS. Direct observations of zooplankton are a rich source of

information on ecosystem state and of how pelagic ecosystems respond to climate forcing.[8] This is true for several reasons. First, because most zooplankton have short life cycles (weeks to months), their population dynamics are tightly coupled to physical variability and environmental change. Second, given their role in food webs as consumers of primary production and prey for fish and higher trophic levels, changes in zooplankton species composition or community structure can serve as a robust index of climate-driven changes in ecosystem structure. Third, many zooplankton species are so-called "indicator species", the presence of which in a zooplankton sample is nearly as accurate as physical data in telling us the source of water that has been sampled (and, thus, the influence of large-scale transport processes).[9] Finally, zooplankton are very abundant and readily quantified using relatively simple methods.

Despite the high information content of zooplankton observations, such data are remarkably sparse in space and time when considered in the broad context of OOS as a whole. At present, some of the longest times series of zooplankton data are based on plankton net samples collected over the course of infrequent (e.g., three or four times per year), quasi-synoptic surveys (e.g., CalCOFI off southern California,[10] IMECOCAL off Baja California, Mexico,[11] and Line P off Vancouver Island, Canada[12]) or from relatively frequent (i.e., monthly) occupation of a station deemed representative of a large region of interest (e.g., the Hawai'i Ocean Time-series (hahana.soest.hawaii.edu/hot) and the Bermuda Atlantic Time-series Study (bats.bios.edu)). In this context, we argue that high-frequency coastal transects (HFCTs) have an essential role in a comprehensive OOS, and that this role will likely continue well into the future even as advanced technologies for autonomous sampling continue to develop and be implemented in the field. We base this argument on our experience with sampling along such lines in the northern California Current (NCC) and bringing these data into coast-wide syntheses of the California Current Ecosystem (CCE)[13] and the California Current Integrated Ecosystem Assessment (CCIEA; www.noaa.gov/iea/regions/california-current-region/index.html). However, we expect that many of the themes we touch upon next will apply to similar efforts in other coastal regions and provide strong motivation for establishing such lines in a coast-wide network.

2. HIGH-FREQUENCY COASTAL TRANSECTS

High-frequency coastal transects (HFCTs) are ship-based surveys of short transects that span the continental shelf and extend to waters over the upper to mid-slope. Survey cruises are executed rapidly (<12 h) at intervals of two to four weeks throughout the year. HFCTs rely on research vessels of modest size (12−30 m) and running cost ($3000−5000 per day), sailing out of local home ports. Flexibility in vessel scheduling is essential, as it allows HFCTs to be sampled during windows of favorable (or at least safely workable) weather and sea conditions.

In the NCC, opportunities to conduct effective surveys of any sort can be quite limited during the winter storm season and when strong upwelling-favorable winds affect the region during the spring and summer months; yet, we have had good success in maintaining year-round sampling along two HFCTs in this region. We describe these two HFCTs—the Newport Hydrographic Line and the Trinidad Head Line—as examples of what we mean by these sampling protocols and as a basis for highlighting what has been learned from such sampling in the NCC. These HFCTs are separated by about three degrees of latitude (approximately one-fifth of the coastline between Cape Flattery, Washington, and Point Conception, California), and they bracket the northern extent of a transitional zone between the relatively simple upwelling system along Oregon's relatively linear coast and regions south of Cape Blanco where interactions between stronger winds, complex orography, and bottom topography result in stronger mesoscale activity.

2.1 THE NEWPORT HYDROGRAPHIC LINE

The Newport Hydrographic Line (NHL) extends west from Newport, Oregon (44.6°N; Figure 1). This line was first sampled by physical oceanographers from Oregon State University from 1961 to 1973 with support from the Office of Naval Research, directed toward study of the (then) poorly understood hydrography of the northern California Current. From 1969 to 1973, Oregon Sea Grant supported early work on the zooplankton and ichthyoplankton in continental shelf waters along the NHL.[14−16] After 1973, apart from a handful of cruises that sampled zooplankton during the summers of 1976 to 1978, 1983, and 1990 to 1992,[17−19] the NHL was not systematically sampled again until 1996. Since 1996, the inner 40 km of the Newport Line (continental shelf and slope) has been sampled on a fortnightly basis. The offshore extent of the NHL, which extends into oceanic waters 140 km from shore, was sampled quarterly from 1998 to 2005 and two or three times per year since. Sampling along the inner 40 km of the NHL has been supported largely by two vessels, the 12-m *R/V Sacajawea* and the 19-m *R/V Elakha*.

2.2 THE TRINIDAD HEAD LINE

The Trinidad Head Line (THL) extends due west from Trinidad Head (41.05°N; Figure 1) in northern California and is anchored at the coast by a shore station maintained by CeNCOOS and Humboldt State University at Trinidad Wharf. The THL is situated near the midpoint of what was then an extensive latitudinal gap in year-round ocean observing efforts between the NHL in the north, and to the south, the northern lines of the CalCOFI grid, especially CalCOFI Line 67 off Monterey Bay. The THL lies approximately 53 km south of where the Klamath River—a key watershed in management of West Coast salmon fisheries—drains into the Pacific Ocean (approximately 41.54°N). Initial sampling along the THL began in 2006, with consistent monthly (and occasionally biweekly) sampling established in early 2008. Sampling along the THL is supported by Humboldt State University's 27-m *R/V Coral Sea*.
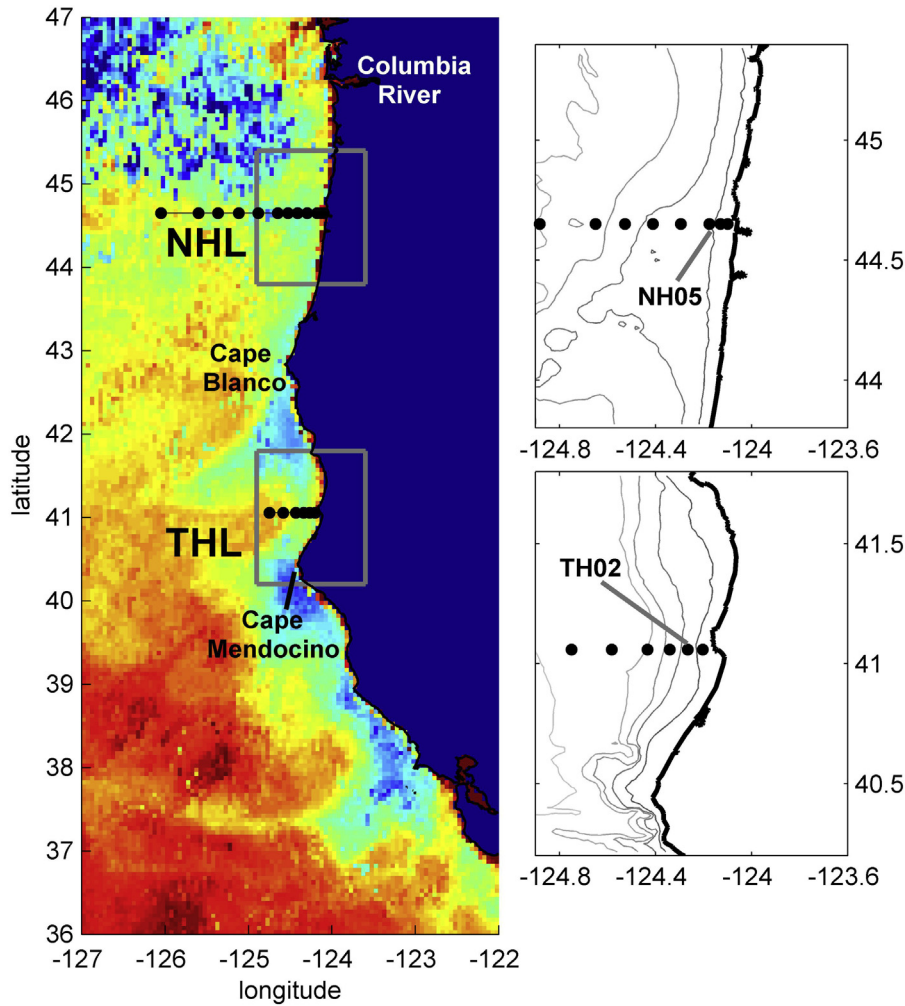
FIGURE 1

Newport Hydrographic Line (NHL) and Trinidad Head Line (THL) overlain on sea surface temperature (eight-day composite centered on 1 June, 2013, downloaded from coastwatch. pfeg.noaa.gov/erddap). Gray boxes indicate location of detailed charts of coastal stations and bathymetry. Contours indicate, in order of dark gray to light gray, 50-, 100-, 200-, 500-, 1000-, and 2000-m isobaths. Observations from highlighted stations are discussed in greater detail in the text.

2.3 SAMPLE COLLECTION AND ANALYSIS

Along both lines, zooplankton are sampled at each station with a 0.5-m ring net fitted with 202-μm mesh and a TSK flowmeter. The net is lowered to a maximum depth of 100 m at deeper stations or within a few meters of the sea floor at shallower shelf stations, then retrieved vertically to the sea surface. These samples are analyzed to quantify the abundance of copepod species, many of which are further identified to stage and sex, euphausiid eggs and larvae, and other zooplankton (see Ref. 20 for further details on methods of analysis). Along the NHL, larger zooplankton (e.g., euphausiids, pteropods, ichthyoplankton, etc.) are sampled at night with 0.5-m diameter Bongo nets fitted with 333-μm mesh towed obliquely through the upper 20 m of the water column. During the quarterly (more offshore) cruises, the Bongo net is fished obliquely to a depth of 100 m. Along the THL, larger zooplankton are sampled with oblique tows of 0.60-m diameter Bongo nets fitted with General Oceanics flowmeters and 505-μm mesh on one side and 335-μm mesh on the other, fished to a maximum depth of 100 m; this allows a greater portion of the water column to be sampled at on-shelf stations that are occupied during daylight on the THL.

Standard in situ observational data are collected during surveys along both lines. CTD casts are conducted at each station to obtain depth profiles of water temperature, salinity, chlorophyll fluorescence, and dissolved oxygen. Bottle and surface water samples are collected for assay of nutrient and chlorophyll concentrations (and phytoplankton species composition along the NHL).

3. WHAT CAN ZOOPLANKTON DATA TELL US ABOUT THE NCC?

The answer to this question lies in understanding what drives variability in copepod communities and recognizing that copepod community structure strongly indexes the ecosystem response to variability in physical forcing. As reviewed below, copepod community data effectively integrates the (often lagged or nonlinear) response of coastal ecosystems to physical forcing acting across a range of spatial and temporal scales.

Why focus on copepods? In part, because copepods are highly abundant and are one of the major links between phytoplankton and fishes in marine food webs. Just as importantly, many of the numerous species of copepod that frequently appear in our samples can be classified according to their affinity for colder versus warmer water and offshore versus neritic habitats.[20,21] The consistency of these affinities underpins the utility of copepod community structure as an indicator of ecosystem state and how the ecosystem is responding to large-scale forcing. Indeed, several individual species are so strongly linked to water masses with particular characteristics that they serve as effective indicators of seasonal changes in circulation patterns, the onset of the upwelling season, oceanographic regime shifts, and potential responses to climate change.[20–23]

Based on analysis of data collected along the NHL and, in particular, the time series of observations of zooplankton at the mid-shelf station NH05 (situated at mid-shelf, approximately 9 km from shore in about 60 m of water, Figure 1), we have documented strong variability in copepod communities off the Oregon coast. Climatologically, cold-water taxa dominate the coastal zooplankton community during the summer upwelling season (typically May through September) when equatorward flow along the coast is fed from northern sources. Conversely, a diverse suite of warm-water taxa is dominant during winter when poleward flows (e.g., the Davidson current) occur. Qualitative differences in the energy content of cold- and warm-water copepods magnify the value of understanding variability in coastal copepod communities as a basis for understanding broader ecosystem dynamics. Specifically, two of the cold-water species, *Calanus marshallae* and *Pseudocalanus mimus*, are rich in lipids relative to warm-water taxa.[24] These differences mean that which species are present has important implications for the bioenergetic content of the food chain and subsequent transfer of energy to higher trophic levels.

3.1 TEMPORAL VARIABILITY: CLIMATE VARIABILITY AND CHANGE

Variability in the annual climatological pattern in copepod species composition at both NHL and THL is linked to variability in large-scale forcing of the North Pacific. In particular, the copepod community off Oregon and northern California is especially responsive to changes in the Pacific Decadal Oscillation (PDO), which indexes changes in the strength of equatorward flow carrying subarctic water into the California Current.[25-27] When the PDO is in negative phase, cold water species are more abundant (and have greater biomass), but when the PDO is in positive phase, warm water species tend to dominate. These patterns appear to be driven by variations in large-scale transport associated with the PDO such that when a greater proportion of the water entering the NCC is from the coastal Gulf of Alaska and the subarctic side of the North Pacific Current, lipid-rich copepods dominate; whereas when the PDO is in positive phase, a greater proportion of water entering the NCC is from the subtropical branch of the North Pacific Current and lipid-poor taxa are more common.[26,27] Similar variability has been documented in response to El Niño (warm) and La Niña (cool) conditions.[28] The response to strong El Niño events is especially profound as El Niño disrupts transitions related to seasonal upwelling and equatorward flow. During such events the abundance of warm-water species is typically greater than normal and the abundance of cold-water species is greatly reduced, regardless of season.[28]

This close coupling between copepod community composition and large-scale forcing associated with the PDO and ENSO presages the ability of HFCTs to detect ecosystem responses to ongoing and future climate change. Trends and shifts in physical conditions will be readily observed by several elements of OOS, but they may not be immediately informative with respect to ecosystem state. In contrast, the arrival of new taxa from southern waters, or the failure of northern

species to return as expected, would be a clear indicator of change with respect to how zooplankton communities (and, by proxy, ecosystem productivity) are shifting north or are otherwise being altered.[29,30] Moreover, HFCTs can reveal zooplankton responses to changes in upwelling intensity or ocean stratification driven by climate change and whether changes elsewhere in the North Pacific affect zooplankton communities that are transported into coastal waters of the CCE.[31,32]

3.2 TEMPORAL VARIABILITY: THE ANNUAL PRODUCTION CYCLE

One of the strengths of HFCTs is the ability to sample throughout the year, taking advantage of sometimes narrow windows of favorable conditions. This has allowed us to develop a broader perspective on when and how production events occur during different parts of the year, and to develop metrics that capture important variability in the annual cycle.

3.2.1 Ecosystem Preconditioning in Winter

Observations along the NHL have allowed us to resolve aspects of variability in the annual production cycle that would be difficult at best to capture with any rigor in quarterly or annual surveys. Several recent studies have elucidated statistical relationships between integrated measures of productivity and ocean conditions during the winter months preceding the onset of the upwelling season.[33–38] Analogous relationships emerge from analyses of recruitment variability in winter-spawning rockfishes (*Sebastes* spp.),[39–41] the young of which serve as important prey for seabirds and larger fishes later in the spring.[42,43] These relationships suggest that enhanced primary and secondary production during winter "preconditions" the ecosystem to respond robustly to upwelling in the spring, which implies that winter forcing has a disproportionate influence on overall annual productivity.

Off Oregon, significant wintertime productivity events depend on two factors. The first is the emergence of *Neocalanus* spp. and *Calanus marshallae* from diapause in early January, which rapidly increases copepod biomass in surface waters.[44] During this time, both *C. marshallae* and *Calanus pacificus* begin to produce eggs using stored lipids and by feeding on ciliate prey. The second factor is the occurrence of conditions that favor a winter phytoplankton bloom.[45] In the NCC, such blooms can occur anytime between late-January and early March, when an extended period of calm winds and clear skies allows phytoplankton to bloom in response to increased light, stratification (reduced mixing), and sufficiently high nutrient concentrations (ca.10 μM nitrate) that have accumulated over the winter months. This "clear sky" event does not occur every year off Oregon; however, when these conditions do occur, the resulting bloom can support higher egg production by copepods and euphausiids and greater growth and survival of their larvae and juveniles.[36,37] The net effect is that winter blooms enhance the ecosystem's potential to respond to the onset of sustained upwelling in spring, and it is thought to be the basis for the statistical relationships described

previously. Off northern California, we have observed distinct winter bloom events, with clear skies coinciding with light upwelling-favorable winds out of the north in January, followed by additional storm activity. These observations contrast with conditions off central and southern California, where late-winter blooms appear to be associated with the onset of the upwelling season, which often (but not always) occurs earlier at such latitudes.[46,47]

3.2.2 Ecosystem Transitions in Spring

Because of the importance of upwelling for enrichment of coastal ecosystems, several indices have been proposed to distill seasonal variability in upwelling and its consequences in the California Current to simpler interannual metrics. Some studies[33,47] have used cumulative daily values of the Bakun upwelling index[48] to estimate date of spring and fall transition, and length of the upwelling season, whereas others used cumulative wind stress from local winds[49] or have focused on changes in sea level at the coast.[50]

These physical indicators, however, are, at best, indirect indicators of ecosystem state, particularly because in many years, when the upwelling season is first initiated, winds often are weak and alternate between southerly and northerly before settling in a persistent pattern of northerly winds. Thus, these indicators and transition metrics do not capture the initiation of biologically significant productivity and, indeed, may be somewhat decoupled from ecosystem responses depending on recent history of the system. For example, during the El Niño event of 1998, upwelling was quite strong, but the waters that upwelled were warm and nutrient poor, having been drawn from above a depressed pycnocline, and productivity was not enhanced (discussed in Ref. 28). In 2005, upwelling was delayed (spring transition date estimated 24 May, nearly six weeks after the climatological mean) but a significant amount of upwelling did not begin until an additional six weeks had passed (12 July). This caused a complete collapse of the normal upwelling-fueled food web and high mortality of juvenile salmon that went to sea that spring and summer, with the end result that returns of salmon two−three years later were so poor that the salmon fishery along the West Coast of the United States was closed for two years.[51] This event also led to recruitment failures in rockfish stocks and poor reproductive success in many seabirds.[52,53]

Direct observation of upwelling and its consequences can improve the utility of indices based on "date of spring transition" for resource managers. This has been done using NHL CTD data to define the "physical spring transition" as the date on which water colder than 8°C is first observed near the sea floor in mid-shelf waters. This definition effectively integrates physical processes leading to the presence of cold, nutrient-rich water that will upwell at the coast with the onset of strong northerly winds and, thus, indicates conditions favorable to high plankton production rates. In years where shelf waters remain warm, as can occur during strong El Niño events, it is possible that this threshold might never be achieved and no transition to upwelling defined. We define an analogous "biological spring transition" as the date when the copepod community has transitioned from the winter
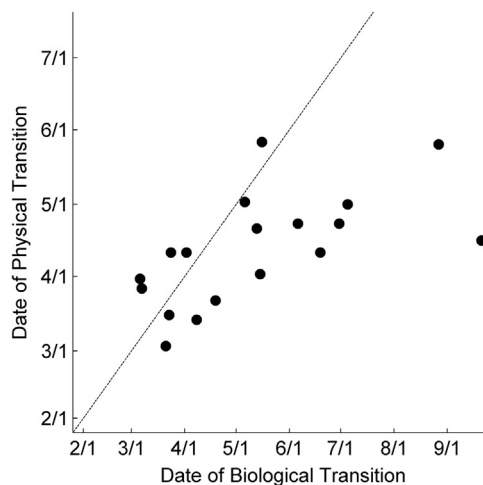
FIGURE 2

Comparison of date of biological transition based on appearance of cold-water copepod taxa along the Newport Hydrographic Line and the date of spring transition based on physical observations using the definition developed by Logerwell et al.[33] Dashed line is 1:1 relationship to illustrate progressive delay of biological transition when physical transition occurs later in a given year.

warm-water community to a summer cold-water community. Corresponding indices of "fall transitions" marking the end of the productive upwelling season are based on displacement of cold bottom water from the shelf and the disappearance of cold-water copepod communities.

Comparisons to physical indices of spring transitions, such as that proposed by Logerwell et al.[33] illustrate why transition indices based on copepod species abundance data are more useful information for fisheries management. When upwelling begins early in the year (up to day 100 or mid-April), cold-water copepods arrive at approximately the same time, and physical and biological definitions of the spring transition are in general agreement (Figure 2). However, if the physical signs of upwelling appear later in the year, biological responses are disproportionally delayed (Figure 2). This disparity underlies the value of direct biological sampling, as physical indices alone are not effective predictors of ecological conditions, especially in unusual years such as 1998 and 2005.

3.2.3 Upwelling and Productivity

Results from several process studies and research programs, including the NHL time series, have given us a relatively good understanding of production associated with the upwelling season off Oregon. The "spring transition" (typically in April or May) is marked by the onset of sustained upwelling that fuels a burst of primary and secondary production, and strong upwelling events occur at five to 10 day

intervals during the peak of the upwelling season (July to August), resulting in dense phytoplankton stocks. These blooms support massive egg production by the euphausiid *Euphausia pacifica*[36] and maximum egg production rates in *Calanus marshallae*, *Pseudocalanus mimus*, and *Acartia longiremis* (Refs. [54,55] and Peterson *unpublished data*).

3.2.4 Fall Blooms

Year-round sampling along the NHL has allowed us to characterize the occurrence of fall blooms as well. These blooms usually occur in October, in response to stratification and clear skies after the first major storms of the season mix the water column and raise nutrient concentrations near the surface. Following this bloom, southwesterly storms, deep mixing, and reduced insolation prevent any substantial productivity through the late autumn and early winter. The broader implications of such blooms for ecosystem productivity in the CCE are not well understood.

3.3 SPATIAL VARIABILITY: ALONGSHORE COHERENCE AND DECOUPLING

The insights reviewed above are grounded in nearly 20 years of continuous observations along the NHL (primarily at the single station NH05), augmented by historical data from the 1960s and 1970s. However, looking more broadly at the CCE, questions remain regarding how well observations off Newport capture variability in the broader CCE, and even when correlations exist, what are the mechanistic links that underlie the observed relationships? Or, considering part of the motivation for initiating the THL, can we develop similar insights to ocean influences on survival of Klamath River fall-run Chinook salmon (*Oncorhynchus tshawytscha*), one of the linchpin stocks for salmon management along the US West Coast? While we are not yet to the point of addressing these broader questions in a deeply informative way, the time series of copepod community data along the THL has matured sufficiently to allow us to explore how copepod communities vary over time and space over three degrees of latitude within the NCC.

To illustrate the potential insights to be gained from analysis of data from the two HFCTs, Figure 3 shows an ordination based on nonmetric multidimensional scaling (NMDS) of log-transformed copepod abundance data collected at mid-shelf stations (TH02 and NH05) along each transect from 2008 to early 2014. The two stations are both about 9 km offshore; the depth at TH02 is 75 m and at NH05, 60 m. To better balance the data set, NH05 data were thinned to include only those samples that occurred within a few days of a corresponding sample at TH02 (see Refs. [26,52] for description of ordination methods). This ordination indicates substantial separation between the copepod communities observed at NH05 and TH02, structured by variability in the abundance of species with cold-water, neritic affinities versus those more commonly found in warm-water, oceanic habitats (NMDS1) and the abundance of cold-water, oceanic (subarctic) species relative to warm-water, neritic species (NMDS2) (Figure 3). Differences between the two copepod communities
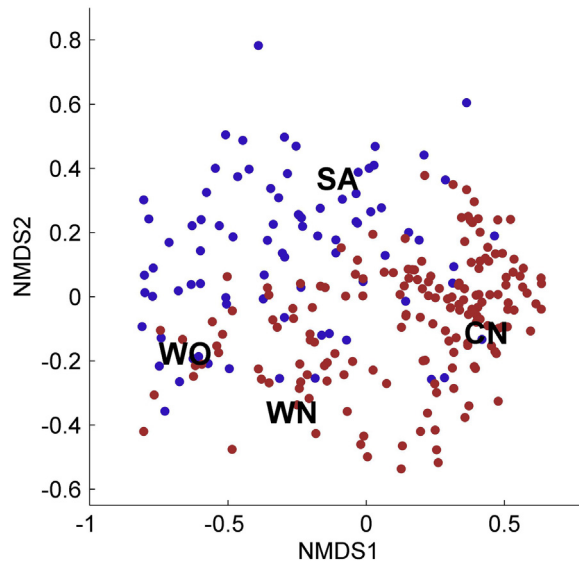
FIGURE 3

Results from NMDS ordination of copepod community data from station TH02 along the Trinidad Head Line (blue) and NH05 along the Newport Hydrographic Line (red), showing the position of individual observations and the mean position of copepod taxa with cold-neritic (CN), subarctic (SA), warm-neritic (WN), and warm-oceanic (WO) affinities (following Ref. 21).

persist throughout the seasonal cycle, with the assemblage off Oregon tending to include more nearshore species, and the assemblage off northern California having a stronger oceanic component.

This preliminary comparison highlights the value of networked HFCTs, as the lipid-rich copepods that commonly dominate off Oregon during cool, productive conditions are not as common off northern California, even though we expect to see similar shifts in ecosystem productivity through the course of the annual cycle. Moreover, this comparison also suggests that the two regions experience climate variability in different ways: following the decay of the 2009–2010 El Niño event, the abundance of cold-water neritic species recovered slowly off Oregon, whereas the copepod community off northern California was dominated by more offshore, subarctic species. Ongoing work is focused on understanding how differences in local environmental conditions, local bathymetry (e.g., retention), and circulation patterns might contribute to these differences, motivated in part by the potential for insight to drivers of alongshore variability in marine survival of salmon stocks.

3.4 SPATIAL VARIABILITY: CROSS-SHELF ZONATION AND HYDROGRAPHIC STRUCTURE

In our review thus far, we have focused on indices derived from data collected at a single mid-shelf station along each of the two transects, however, HFCTs provide these data in the context of nearly synoptic observations of hydrography and plankton ecosystem characteristics across the shelf and upper slope. For example, during the upwelling season off Oregon, we observe the following set of assemblages structured by hydrography and circulation[54,56−59]:

- A unique assemblage of zooplankton in the nearshore zone (the inner 5 km) composed of the larvae of benthic invertebrates (barnacles, bivalves, and several crabs) and copepods (*Acartia hudsonica* and *Centropages abominalis*)
- A high-biomass, low-diversity assemblage dominated by *Pseudocalanus mimus*, *Calanus marshallae*, and *Acartia longirmis* and the eggs and larvae of euphausiids in mid- to outer-shelf waters
- A low-biomass, high-diversity, oceanic assemblage of subtropical and transition zone species offshore of the shelf break

Moreover, cross-shelf sampling yields data on the several euphausiid taxa, including *Thysanoessa spinifera*, which can be highly abundant just inshore of the shelf break, especially in years with a winter "clear sky" bloom,[36] and *Euphausia pacifica*, the dominant grazer and producer at the shelf break and offshore. The presence of other euphausiids (e.g., *Nyctiphanes simplex* and *Stylocheiron* spp.) or other taxa (e.g., *Emeritia* larvae) can corroborate information on transport inferred from copepod community data.[60,61] Sampling along HFCTs has also supported analysis of variability in larval fish community structure and abundance.[62,63]

Integration of cross-shelf data into indices and management has not been well developed as it has for mid-shelf stations that capture conditions that strongly influence important fisheries resources (e.g., salmon and rockfish). Nevertheless, through these observations, HFCTs enrich OOS with information on conditions affecting several parts of the ecosystem, and how cross-shelf zones respond to variation in local- and basin-scale forcing, both directly and in connection to other zones. For example, comparisons along the NHL have documented lower variability in copepod communities in waters over the slope relative to those observed in the more dynamic shelf waters.[64] HFCTs allow us to observe other processes as well, such as the consequences of ongoing acidification of ocean waters and upwelling of deep corrosive waters through analysis of pteropod shell dissolution along cross-shelf gradients of ocean pH,[65] and to develop inferences regarding transport of coastal zooplankton and invertebrate larvae.[66,67] In our ongoing work, we are expanding the data available for offshore stations of the THL and integrating these data to enrich elements of the CCIEA focused on the NCC.

4. ZOOPLANKTON-BASED ECOSYSTEM INDICATORS

From a more applied, informational perspective of OOS, zooplankton data are the basis for several prominent ecosystem indicators included in the CCIEA. Data from the NHL contribute to several indicators for the NCC, including the following:

- Northern Copepod Biomass Anomaly, which is considered as a proxy for the amount of wax esters and fatty acids available to higher trophic levels, and especially to several pelagic fish species for which these energy sources are critical to overwinter growth and survival[20]
- Southern Copepod Biomass Anomaly, an indicator of poleward, onshore transport that displaces productive, lipid-rich copepod communities[20]
- Copepod Species Richness, which captures transitions between relatively species-poor, but productive cold-water communities and the more diverse, less productive warm-water communities[23]
- Copepod Community Index, which is derived from nonmetric multidimensional scaling (NMDS) and highlights variability between cold water, neritic communities, and other less productive ecosystems[26,68]

Of these, Northern Copepod Biomass Anomaly and Copepod Species Richness have proven to be among the most informative of the 40 or so indices considered for the NCC.

Hydrographic and zooplankton data collected from the NHL and THL are analyzed rapidly after each cruise, so that the zooplankton (and transition) indices are updated in timely fashion for resource managers focused on forecasting the status of harvested stocks or evaluating ecosystem state. One prominent example of how data from an HFCT directly informs management can be found in the use of observations from the NHL to generate forecasts for salmon returns to coastal watersheds in Oregon and to the Columbia River.[7,69] This information is obviously useful in the management of fisheries, as managers and fishers peer into the future as part of their regulatory processes and strategic planning. This information is also valuable for evaluating watershed and land-use management activities and hatchery practices that affect production and survival of juvenile salmon in freshwater habitats. Specifically, zooplankton-based indices help to account for variability in marine growth and survival in evaluating whether changes in freshwater habitats have a beneficial or detrimental effect on salmon populations.

In particular, the northern copepod index during the year that juvenile salmon go to sea appears to be a relatively good predictor of salmon returns one to two years later (e.g., Figure 4). These relationships support the hypothesis that salmon survival is enhanced by the presence of a lipid-rich cold-water copepod community in coastal waters. The link between copepods and salmon is almost certainly through the food web, as juvenile Coho and Chinook salmon prey on euphausiids and small fishes rather than directly on copepods. We suspect that cold-water copepods serve as a proxy for the abundance of cold-water coastal fishes such as herring, smelt, and sand lance, as well as being lipid-rich energy sources directly available to these
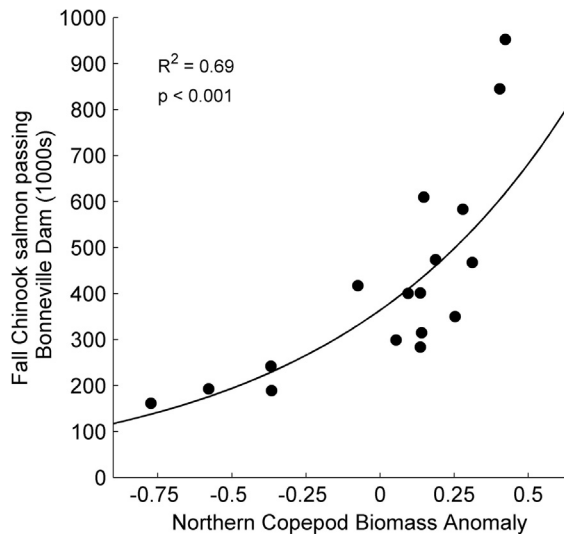
FIGURE 4

Relationship between northern copepod biomass anomaly[21] and returns of fall-run Chinook salmon past Bonneville Dam two years later, illustrating predictive power of zooplankton indices for salmon forecasts. Counts of fall-run Chinook include both lower-river "tules" (believed to be mostly fish that have spent two years at sea) and upriver "brights" (believed to be mostly fish that have spent three years at sea).

planktivorous fishes and to larval fishes that also comprise a substantial portion of juvenile salmon's diets.

5. DISCUSSION

The blend of scientific insights and ecosystem indicators reviewed in this chapter are the result of old-fashioned approaches to ocean observing—going out to sea on a regular and frequent basis to sample the system as holistically as practicable using relatively simple methods. Perhaps the most unique and powerful lesson to be taken from this work is the clear demonstration that zooplankton community data offer greater explanatory power and potential for direct societal benefit (through better informed management) than do physical observations or indices several steps removed from species with high commercial or conservation value. More specifically, the power of zooplankton data emerges largely from knowing what species are present, with the impact of variability in community composition magnified by ecologically significant differences in energetic content among groups with different biogeographical affinities. By demonstrating differences in food chain structure related to climate forcing (especially the PDO), our work lays out a strong

hypothesis that links basin-scale climate variability to the local dynamics of sardine, anchovy, and salmon. To develop these indices further, we are developing lipid content time series for key taxa along both lines to examine how lipid content differs seasonally and alongshore.

Moreover, by adopting a strategy that contrasts sharply with infrequent, large-scale hydrographic surveys, HFCTs have allowed us to characterize seasonal variability in production, even during winter periods that present logistical challenges for sampling and had been widely believed to be unproductive. Through this work, we have shown that Oregon waters can be productive from January through October, not just during the April—September upwelling season. Similar observations are emerging from sampling off northern California. Thus, HFCTs can help to resolve variability in the occurrence and timing of production events, as well as their magnitude and duration, all of which are highly informative for understanding ecosystem state and variability in higher trophic levels.

5.1 HFCTs, ADVANCED TECHNOLOGIES, AND BIOLOGICAL SAMPLING IN OOS

Extracting zooplankton community data from zooplankton samples is labor intensive and requires substantial taxonomic expertise, yet this effort is critical to the value of these time series. Yet, had we only a time series of aggregate density measures based on counts or biomass of undifferentiated zooplankton, or volume of entire samples, we would lack the ability to develop insights into the differences in the copepods seen with season, cross-shelf, or alongshore and how these differences correlate with the recruitment dynamics of fishery stocks and other species of interest.

At present, automated sampling technologies and autonomous sampling platforms show great promise, but they have not developed sufficiently to fully supplant at-sea sampling followed by careful microscope work. Indeed, the full extent and richness of the data described here—and the indicators derived from these data—cannot yet be collected in any other way. Optical particle counters can return data on fine-scale patchiness and size distributions in plankton distributions, and biomass can be estimated from the size and number of particles observed in a tow, yet such data have relatively low information content compared to a data set on abundance and biomass resolved to the species level. Optical instruments yield sharp images of individual zooplankters in situ, yet the ability to process voluminous imagery data efficiently, and in particular to discriminate similar species, presents ongoing challenges.[70,71] Genetic techniques hold great promise as approaches for identifying species present in a sample and their relative abundance.[72] Coupled with optical (or other) measurements, genetic analysis of individual zooplankton has the potential to support automated identification of zooplankton by species and developmental stage and, thus, estimation of species-specific biomass. We can imagine automated assays that augment taxonomic data with estimates of energy available to higher trophic levels; however, such technologies still lie well into the future. Acoustic techniques yield information on the distribution and (relative) abundance of selected classes of

"echo-targets," yet still require "net-truthing" of what is being quantified and to collect information on diversity.[73,74] Clearly, OOS will benefit greatly from successful research and development of automated technologies and their deployment on autonomous sampling platforms, but much work remains to be done before ship-based surveys are supplanted if detailed data on zooplankton and highly informative zooplankton-based ecosystem indicators are to continue to be available to managers.

5.2 CHALLENGES IN IMPLEMENTING HFCTs AS ELEMENTS OF OOS

Several challenges arise in implementing or maintaining HFCTs as part of an OOS. Like any other element of an OOS, there is an up-front investment in personnel and equipment to stand up a new HFCT, and many of these expenses (ship time, personnel) are ongoing. Another ongoing challenge is maintaining excellent access to locally based coastal research vessels of small-to-moderate size. To be effective, HFCTs must operate with sufficient frequency to remain "priority customers" for vessels, as rare, short cruises will not suffice to warrant a dedicated UNOLS-class vessel, yet competition with other users for local vessels can make it difficult to maintain flexible scheduling in response to variable weather conditions. Under most conditions, larger oceanographic research ships cannot carry out this work cost-effectively, whether because they hail from distant homeports or they are over-kill as a platform for this relatively simple observational work. Fortunately, as our experience demonstrates, the smaller vessels ideal for HFCTs also can serve as platforms capable of supporting concurrent (leveraged) research, ancillary observations, technology development, and training.

A second challenge is developing and supporting staff with substantial taxonomic expertise and coordinating this expertise and methodology across HFCTs. Efficient extraction of information from plankton samples requires the dedicated effort and careful attention of para- and master taxonomists.[70,75] Training of taxonomists is a serious investment of time and resources—particularly for challenging taxa such as copepods—yet it remains essential for maintaining ongoing time series and to support the development of reliable automated methods.

A third challenge arises from variability in sampling protocols. Comparisons among disparate sampling programs often requires distillation of each data set to anomalies,[8,76] yet it can be difficult to establish that such measures are indeed comparable. Early in the course of establishing the THL, we implemented the vertical ring-net sampling protocol used on the NHL—the same methods endorsed and used by the U.S.GLOBEC program—to ensure comparability of the two data sets. In contrast, our Bongo sampling protocols have remained slightly different, based on differences in sampling goals.

A fourth challenge in establishing new HFCTs is that zooplankton data may be of limited use until a sufficient time series has been established. In contrast to remote sensing technologies that more or less immediately provide a product useful to OOS missions (e.g., a new HF radar site enhancing search-and-rescue and spill-response capabilities), developing ecosystem information from a new

HFCT may require several years of observation. Insights and indices from the NHL time series are based on nearly 20 years of observation, and they clearly demonstrate the value of long observational time series essential for understanding climate—ecosystem dynamics.[77] Observations along the THL have been integrated in several annual synthesis reports on the California Current since 2008, and they provided useful comparisons to observations to the north (especially the NHL) and to the south (see, e.g., Refs. 78,79). Now, as it approaches seven years in length, the THL time series can support rigorous assessment of variability in zooplankton communities of the NCC, but several more years will be required before comparisons to the dynamics of local salmon stocks (e.g., Klamath River Chinook salmon) can be developed with any rigor. We are now actively engaged in developing indices based on observations from the THL for integration in the CCIEA, but this effort was not considered warranted for the first six years of the THL.

5.3 OPPORTUNITIES AND THE ROLE OF HFCTs IN OOS

If these challenges continue to be met, HFCTs will continue to enhance the information available to OOS, as clearly demonstrated by the ecosystem indicators incorporated in IEAs and in the information available to fisheries managers, and to support efforts on several fronts directed at advancing our understanding of marine ecosystem dynamics and informing management. Based on past data, and indeed, going forward, HFCTs have a role in outlining the range of information that developers of autonomous systems should strive to capture and are well situated to collaborate in this development. Moreover, the data returned by HFCTs are of great value to the modeling community as it advances the frontier of dynamic models beyond realistic representation and forecasting of the physical system to models that achieve greater realism in ecosystem dynamics. Resolving zooplankton (and in some cases phytoplankton[80]) to species provides opportunities for developing and evaluating models that seek to account for importantly differing biological groups within trophic levels as part of the dynamics of the system (e.g., Refs. 81,82).

HFCTs represent one solution to the tradeoff that faces all OOS—synopticity, spatial extent, temporal resolution, and parameter coverage. Thus, even as HFCTs fill a critical gap in ocean observing, rigorous analysis of variability in zooplankton communities and its causes depends on environmental data from other elements of OOS. Indeed, our own ongoing work to understand the dynamics of copepod communities and populations draws on environmental time series and circulation models that assimilate a diverse suite of ocean data.

Our work in the NCC points to the value of networked HFCTs for understanding ecosystem dynamics, particularly in a complex system affected by strong environmental gradients such as the CCE. It is possible to demonstrate significant statistical correlations between indices based on observations along the NHL and other measures of productivity in the CCE. Yet, without observations from the THL (and ideally other points along the coast), it is difficult to evaluate

similarities and differences in the mechanisms that translate changes in physical forcing to the ecosystem. Moreover, distributed HFCTs can elucidate local responses to large-scale phenomena, as illustrated by differences in recovery of copepod communities during the decay of the 2009–2010 El Niño. This sort of information may help to understand spatial variability in marine survival of salmon and recruitment to other fishery stocks. More generally, data emerging from networked HFCTs will support efforts to extend our empirical, mechanistic understanding of the interplay between local and larger scale processes in ecosystem responses to climate forcing. Previously developed proposals for OOS have called for establishment of HFCTs at several points along the US West Coast, from the Washington coast south to at least Morro Bay, California (to abut the northern extent of the core CalCOFI region), to resolve temporal variability and spatial structure in zooplankton communities, and to understand how local and regional forcing structure productivity in this highly dynamic ecosystem. Placement of future HFCTs should take into account several factors, both logistical (e.g., locations of ports, vessels, and supporting institutions) and ecological (e.g., placement relative to headlands that structure circulation patterns and zooplankton communities,[83,84] and environmental or biogeographic gradients).[85] Insights emerging from the existing pair of HFCTs, including their contributions to understanding larger scale regional variability in the CCE,[13,53,79] argue strongly for implementing such programs as part of a more comprehensive, biologically informative OOS.

Last, we would emphasize that the value of HFCTs is not entirely in the time series and indices produced, but stems also from the simple opportunity to be at sea observing the environment directly. Such experiences are clearly important for engaging students and training young scientists in the field, but they remain valuable to more seasoned researchers as well. Just as fishers have a sense of the ocean born of experience and close interactions with the environment, it is important that we also strive to maintain this contact, pay attention to noticing something new or unusual that we might otherwise not think to sample, and be open to opportunities for developing new lines of inquiry.

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Coastal Ocean Observing Systems

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