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Cross-shelf distribution of copepods and the role of event-scale winds in a northern California upwelling zone

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Abstract

Cross-shelf distribution and abundance of copepod nauplii and copepodids were measured during three summer upwelling seasons (2000–2002) in a coastal upwelling zone off northern California. These 3 years varied considerably in the intensity of winds, abundance of chlorophyll, and water temperature. The cruises in 2000 were characterized by relaxation conditions, with generally high levels of chlorophyll and high water temperature. The cruises in 2001 and 2002 were dominated by strong and persistent upwelling events, leading to lower chlorophyll and water temperatures. The copepod assemblage was dominated by *Oithona* spp., *Acartia* spp. and *Pseudocalanus* spp., with *Metridia pacifica* (*lucens*), *Microsetella rosea*, *Oncaea* spp. and *Tortanus discaudatus* also common during all 3 years. The cross-shelf distribution of copepods was generally shifted offshore during upwelling and onshore during relaxation events, although some variability between species occurred. Abundance of all life stages generally exhibited a negative correlation with cross-shelf transport averaged over at least 1–4 days and lagged by 0–3 days, indicating lower abundances during and immediately after active upwelling. However, copepod nauplii seemed to respond positively to wind events lasting 1–5 days followed by a period of relaxation lasting 6 or 7 days. These rapid rates of change in abundance are probably too great to be due to in situ growth and reproduction alone; physical processes must also play a role. These results suggest a highly dynamic relationship between copepods and upwelling events off northern California, with species-specific responses to upwelling to be expected.

Keywords: Copepods; Nauplii; Cross-shelf transport; *Oithona* spp.; *Microsetella rosea*; *Oncaea* spp.

1. Introduction

The continental shelf off central and northern California is characterized by a strong eastern boundary current (the California Current) and seasonal winds. In the spring and summer, the area is dominated by equatorward winds that result in coastal upwelling and offshore movement of surface waters via Ekman transport, bringing colder and

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nutrient-rich waters into the system. Periodic reversals of these winds can lead to downwelling conditions. The interplay of currents, reversing winds, offshore and onshore Ekman transport and varying coastline geometry creates complex patterns of water movement and ephemeral physical conditions, which in turn affect the organisms in the system.

The California Current system exhibits the high productivity at lower trophic levels that is typical of upwelling systems; it is rich in phytoplankton and zooplankton, especially during the active upwelling season. Copepods are an abundant component of the system biota and it is generally accepted that the events set in motion by coastal upwelling (addition of nutrients, increase in phytoplankton) result in increased copepod abundance. Planktonic organisms in the system are subject to alongshore and cross-shelf advection and their populations might be expected to move across the shelf according to the onshore–offshore water movement associated with coastal upwelling.

Numerous studies have examined the cross-shelf distribution of copepods during general upwelling conditions (Peterson et al., 1979; Verheye and Hutchings, 1988; Escribano and Hidalgo, 2000; Keister and Peterson, 2003; Morgan et al., 2003; Lamb and Peterson, 2005) with varying results. Some reported that upwelling had no effect on cross-shelf copepod distribution (Bernal and McGowan, 1981; Cross and Small, 1967). Others have investigated the behavioral mechanisms copepods might employ in order to avoid being advected beyond the shelf and out of the rich system, such as diel vertical migration (Smith et al., 1981a; Wroblewski, 1982; Batchelder et al., 2002), ontogenetic vertical migration (Verheye et al., 1992; Slagstad and Tande, 1996; Peterson, 1998) or both (Verheye et al., 1991; Verheye and Field, 1992). However, these studies focused on the overall pattern of offshore movement of surface water associated with upwelling. Models have shown that constant upwelling winds cannot explain the high productivity of upwelling systems or correlate to shelf retention of plankton (Wroblewski, 1980; Botsford et al., 2003). However, not much is known about the cross-shelf distributions of copepods as affected by water movement induced by much shorter-scale (several days) wind events. Such events may significantly influence copepod population distributions and abundances over the shelf. Smith et al. (1981b), for example, demonstrated that patterns of zooplankton composition and biomass can be significantly affected by cross-shelf advection fluctuations on a smaller (i.e. daily) time scale, and Dorman et al. (2005) recently examined this phenomenon in relation to euphausiids.

Additionally, it may be important to examine the role of not only those wind events that induce upwelling, but also relaxation from upwelling and even those wind events that lead to downwelling. For instance, despite high nutrients in the upwelling zone off northwest Africa, Jones and Halpern (1981) found that primary productivity remained low during upwelling winds until wind strength decreased. Similarly, Smith et al. (1986) reported that numbers of zooplankton taxa and individuals actually decreased as upwelling intensity increased, and found that copepod nauplii abundance increased during active downwelling. Peterson et al. (1988) found that several copepod taxa off the coast of Chile were low in abundance during active upwelling and higher during relaxation. Similar issues have been addressed with respect to meroplankton off the coast of northern California by Wing et al. (1995).

In the California Current system, periods of strong, equatorward alongshore winds that result in active upwelling are interspersed with winds of variable direction, strength and duration, leading to relaxation or downwelling. The interaction of upwelling favorable events and relaxation or downwelling conditions on very short time scales (i.e. event scales defined by individual wind "events") may have profound impacts on the biota in the upwelling zone. Our objective was to understand the relationship between event-scale winds and the distribution and numerical response of copepod populations. To achieve this, we recorded hourly wind data and repeatedly collected copepods from a cross-shelf transect during three upwelling seasons. By considering specific wind events in conjunction with the cross-shelf distribution and abundance of various life stages of several taxonomic groups of copepods, we examined not only the movement of copepod populations across the shelf, but also their relationship and numerical response to individual upwelling and relaxation events.

2. Materials and methods

Wind and sea-surface temperature data were obtained from the National Data Buoy Center (NDBC). Chlorophyll, copepod nauplii and