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DEEP-SEA RESEARCH Part I

Deep-Sea Research I 54 (2007) 2145-2169

www.elsevier.com/locate/dsri

Interannual and geographical variability of the brood size of the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* along the Oregon coast (1999–2004)

Jaime Gómez-Gutiérrez^{a,*}, Leah R. Feinberg^b, Tracy C. Shaw^b, William T. Peterson^c

^aCollege of Oceanic and Atmospheric Sciences, Oregon State University, 104 Ocean Administration Building, Corvallis, OR 97331-5503, USA ^bCooperative Institute for Marine Resources Studies, Hatfield Marine Science Center, 2030 South Marine Science Drive, Newport, OR 97365, USA

°NOAA/NMFS, Hatfield Marine Science Center, 2030 South Marine Science Drive, Newport, OR 97365, USA

Received 30 June 2006; received in revised form 5 September 2007; accepted 11 September 2007 Available online 19 September 2007

Abstract

Brood sizes of 1259 adult female Euphausia pacifica and Thysanoessa spinifera were measured during 48 h incubations (10 °C, +0.5 °C) on 27 oceanographic cruises between July 1999 and September 2004. The data set includes measurements from several stations off Newport, Oregon (Newport Hydrographic line, 44°39'N) made over a 5-year period and measurements from 14 more extensive cruises at stations representative of continental shelf, slope, and oceanic waters off Oregon and California, USA. E. pacifica had similar brood sizes at inshore (<200 m) and offshore (>200 m) stations with an average of 151 and 139 eggs brood⁻¹ fem⁻¹, respectively. T. spinifera brood sizes were considerably higher at inshore stations—particularly at Heceta Bank (44°N) and south of Cape Blanco (42°50'N)—than at offshore stations, 155 and 107 eggs brood⁻¹ fem⁻¹, respectively. Average brood sizes of E pacifica increased during the study period, from 125 (in 2000) to 171 eggs brood⁻¹ fem⁻¹ (in 2003). Average percentage of carbon weight invested in spawning (reproductive effort) was higher in E. pacifica (~14%) than in T. spinifera ($\sim 6\%$), because both species have similar brood size but T. spinifera females are larger than E. pacifica females and produce smaller eggs. Reproductive effort for both species was higher during summer 2002, probably associated with anomalous cool subarctic waters and high chl-a concentration observed during that summer. Brood sizes and chl-a values remained relatively high in 2003–2004 compared to the 1999–2001 period. Geographical and temporal variability in brood sizes for both species were significantly correlated with *in situ* measurements of chl-a concentration but not with sea surface temperature. No gravid females were collected during late autumn and winter cruises, thus the spawning season along the Oregon coast appears to extend from March through September for both species. However, T. spinifera usually starts reproductive activity earlier in the spring (March) than E. pacifica. Both species had their highest brood sizes in summer during the period of most intense upwelling, which is associated with an increase in regional phytoplankton standing stock. Published by Elsevier Ltd.

Keywords: Euphausiids; Broadcast spawning; Broad size; Spawning areas; Upwelling; Oregon coast; USA

0967-0637/\$ - see front matter Published by Elsevier Ltd. doi:10.1016/j.dsr.2007.09.003

^{*}Corresponding author. Present address: Centro Interdisciplinario de Ciencias Marinas, Departamento de Plancton y Ecología Marina, Av. IPN, Col. Palo de Santa Rita s/n, AP 592, CP 23096, La Paz, Baja California Sur, México. Tel.: + 52 612 123 4666; fax: + 52 612 122 0350.

E-mail addresses: jagomezg@ipn.mx (J. Gómez-Gutiérrez), Leah.Feinberg@oregonstate.edu (L.R. Feinberg), Tracy.Shaw@oregonstate.edu (T.C. Shaw), Bill.Peterson@noaa.gov (W.T. Peterson).

1. Introduction

Euphausia pacifica and Thysanoessa spinifera are the two most abundant species of euphausiids in the eastern North Pacific, particularly along the shelf break and in the coastal waters off British Columbia, Washington, Oregon, and northern California (Tanasichuk, 1998a, b; Marinovic et al., 2002; Lu et al., 2003; Gómez-Gutiérrez et al., 2005). They are important prey items of Pacific hake (Merluccius productus), mackerels (Trachurus symmetricus, Scomber japonicus), spiny dogfish (Squalus nacanthias) and five species of adult salmonids in this region (Brodeur and Yamamura, 2005; Emmett et al., 2006). In 1997, the US GLOBEC program selected these two euphausiid species for detailed study of their bioenergetics and population dynamics because of their impact as grazers and secondary producers in neritic and oceanic zooplankton communities of the northern California Current upwelling ecosystem. We have been studying their distribution, abundance, and vital rates with the goal of developing an understanding of the life history, larval recruitment, and population dynamics of these two numerically dominant euphausiid species. Egg production rates (eggs brood⁻¹ fem⁻¹d⁻¹) are challenging to estimate because they are highly variable and it is difficult to accurately estimate the interbrood period (IBP), which can range from 2 to 34d or longer for E. pacifica (Gómez-Gutiérrez, 2003; Pinchuk and Hopcroft, 2006; Feinberg et al., 2007). Here we focus on brood size and reproductive effort because they are valuable proxies of the potential recruitment of new individuals to the population. Brood size $(eggs brood^{-1} fem^{-1})$ is an indicator of how much energy a female is devoting to reproduction at the time of collection, and the weight of eggs in a brood, expressed as a proportion of female weight, serves as an indicator of the size-specific reproductive effort by each female per spawning event. Other sensitive reproductive variables are the embryo. chorion diameters, and the perivitelline space (PVS, the difference between chorion and embryo diameters) since these are associated with the egg volume and reflect the amount of energy available for the hatched embryo before it must feed (Ross and Quetin, 1989; Timofeev, 2000; Timofeev and Sklyar, 2001; Timofeev et al., 2004). The ED is likely to be the best indicator of the energy available for embryonic development since the fluid in the space between the embryo and the

chorion is probably not a significant source of organic matter that could be used for growth or metabolism of the embryo. The PVS is also a sensitive index of how embryos respond to temporal and geographical environmental conditions, being usually larger under stressing environmental conditions (Timofeev, 2000; Timofeev and Sklyar, 2001; Timofeev et al., 2004).

The spawning season is usually deduced from the presence of euphausiid eggs or early larval stages in the water column. Along the Oregon coast, eggs and larvae are commonly found in plankton net samples from March through September with highest numbers usually in July and August. Spawning during spring of most years appears to be dominated by T. spinifera (Feinberg and Peterson, 2003; Gómez-Gutiérrez et al., 2005). Two studies have deduced E. pacifica spawning periods from status of female gonad development (Ross et al., 1982; Gómez-Gutiérrez, 2003), but no gonad maturation study has been done for T. spinifera. E. pacifica has a latitudinal cline in the length of the reproductive season, being shorter in duration at high latitudes like in the Gulf of Alaska (July-October) (Pinchuk and Hopcroft, 2006), moderately long (spring-early fall) from southern Canada to central California (Smiles and Pearcy, 1971; Ross et al., 1982; Bollens et al., 1992; Mackas, 1992; Tanasichuk, 1998a; Marinovic et al., 2002; Feinberg and Peterson, 2003; Lu et al., 2003; Croll et al., 2005; Dorman et al., 2005) and year round in southern California (Brinton, 1976). So far, no evidence of a latitudinal reproductive cline for T. spinifera has been detected along its distribution range, probably because there have been few studies that characterize its reproductive season. T. spinifera spawning has been observed from April through October in the Gulf of Alaska (Pinchuk and Hopcroft, 2006), British Columbia (Tanasichuk, 1998b), and Oregonnorthern California (Feinberg and Peterson, 2003; Gómez-Gutiérrez, 2002, 2003; Gómez-Gutiérrez et al., 2005).

Several studies of brood size under laboratory conditions have been published for *E. pacifica* (Ross et al., 1982; Iguchi and Ikeda, 1994; Gómez-Gutiérrez et al., 2006; Pinchuk and Hopcroft, 2006; Feinberg et al., 2007) and *T. spinifera* (Summers, 1993; Gómez-Gutiérrez, 2003; Pinchuk and Hopcroft, 2006). The range in brood sizes of *E. pacifica* in the Gulf of Alaska was 16–298 eggs brood⁻¹ fem⁻¹ (Pinchuk and Hopcroft, 2006), considerably smaller than along the Oregon coast

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