

Latitudinal variation in the recruitment dynamics of small pelagic fishes in the western North Pacific

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Received 10 October 2005; accepted 15 February 2007

Available online 24 February 2007

Abstract

The subarctic Oyashio Current flows south-westward and the subtropical Kuroshio Current flows north-eastward in the western North Pacific, converging in the waters off northern Japan to form the Kuroshio-Oyashio transition region. Some small pelagic fishes inhabit the subarctic or subtropical waters, and others seasonally migrate north and south across the major ocean fronts. Environmental conditions in the subarctic and transition waters are variable, whereas in the subtropical Kuroshio waters conditions are relatively stable. Latitudinally different environmental conditions may affect vital parameters and recruitment variability of small pelagic fishes inhabiting the various waters. Pacific saury *Cololabis saira* migrate seasonally from the Kuroshio to Oyashio waters and spawn in the transition waters in autumn and spring and in the Kuroshio waters in winter. During 1990–1999, the coefficients of variation (CVs) of daily growth rates (G) and instantaneous mortality coefficients (M) were large for larvae and juveniles spawned in the northern transition waters, but relatively small for those from the southern Kuroshio waters. The Pacific stock of chub mackerel *Scomber japonicus* spawns in the Kuroshio waters in spring and early summer and migrates to the subarctic Oyashio waters in summer for feeding, whereas the Tsushima Warm Current stock spawns in the East China Sea in spring and fish remain in the subtropical warm waters throughout their lifetime. The Pacific stock had CVs > 100% for the fish aged 0–5 during 1970–2002. In contrast, the Tsushima Warm Current stock had CVs of 34–40% during 1973–2002. Pacific herring *Clupea pallasii*, which inhabits subarctic waters, had CVs of 118–178% for the fish aged 3–8 y during 1910–1954. Japanese sardine *Sardinops melanostictus*, which spawn in the subtropical Kuroshio waters and migrate to the subarctic Oyashio waters in summer for feeding, had CVs > 120% for the fish aged 0–4 during 1976–2003. Contrasting with these subarctic Oyashio associated species, subtropical round herring *Etrumeus teres* had a CV of 26% over the total catch during 1976–2003. For these small pelagic fishes, latitudinal variation in early life parameters and recruitment was evident at the levels of cohorts (*C. saira*), stocks (*S. japonicus*), and species (Clupeidae). Large variations were observed in the subarctic Oyashio and the Oyashio-affected transition waters, whereas relatively stable results were recorded for the subtropical Kuroshio and its branch, the Tsushima Warm Current. Because the cohorts of Pacific saury and stocks of chub mackerel are not genetically distinct, it is likely that the large variability in the northern waters was environmentally induced in these species. The differences in CVs among clupeids are probably the result of differences in specific reproductive strategies and the environmental characteristics of the waters inhabited by the different species. © 2007 Elsevier B.V. All rights reserved.

Keywords: Latitudinal variation; Recruitment; Small pelagic fishes; Subarctic; Subtropical; Transition region; Vital parameters

1. Introduction

East–west comparisons of ecology and population dynamics have been one of the major approaches in

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the study of small pelagic fishes such as sardines and anchovies (Kawasaki et al., 1991; Schwartzlose et al., 1999). One of the major achievements of such studies is the understanding that fish populations fluctuate in response to climate regime shifts and basin-scale structural changes of ocean ecosystems (Chavez et al., 2003). However, the mechanistic processes connecting climate regime shifts with fish population dynamics remain unknown. For example, a precipitous decline in the Japanese sardine *Sardinops melanostictus* population was triggered by recruitment failure in four consecutive years from 1988 to 1991 (Watanabe et al., 1995). These failures were strongly associated with the 1988/1989 regime shift in the North Pacific (Noto and Yasuda, 1999), but it is unknown which processes in the early life history of the sardine were responsible for the recruitment failure. It is also unknown why Japanese anchovy populations increased concurrently with the decline in the sardine population after the regime shift, despite the fact that both clupeoid fishes are zooplankton feeders.

Not all fish populations fluctuate greatly. Some populations are stable for decades and seem to be immune to large-scale changes in climate and ocean environment. Japanese sardines and round herrings *Etrumeus teres* share spawning grounds in the waters off southern Japan (Kubota et al., 1999). Whereas the Japanese sardine experienced rapid resurgence and decline in the 1970s and 1990s, with a historic peak in the 1980s, there have been stable catches of round herring for more than four decades (Watanabe et al., 2001). A comparative study between such variable and stable fish populations may help to determine the mechanistic processes of fish population dynamics.

North–south latitudinal variation in fish population recruitment has been the subject of much debate in the effort to understand the recruitment dynamics of fish stocks under different environmental conditions. Miller et al. (1991) examined coefficients of variation of recruitment (CVR) for 11 stocks from six species of Pleuronectiformes in the western North Atlantic from Pamlico Sound (35°N) to the Gulf of St. Lawrence (48°N). They hypothesised that recruitment levels vary most at the northern edge of the distribution of a given species, least near the centre of the range, and intermediately near the southern edge. Leggett and Frank (1997) examined this ‘species range hypothesis’ using a recruitment time series of 10–45 y for several stocks of four flatfish species ranging from the Bay of Biscay (46°N) to ICES (International Council for the Exploration of the Sea) IIIa (58°N), and concluded that recruitment variation did not exhibit a consistent pattern based on differences in latitude. Philippart et al.

(1998) used a 13–36-y recruitment time series for four pleuronectids and four gadoids in waters from south-western England (50.9°N) to the Skagerrak in the north (58.5°N), but were also unable to detect any correlation between CVR and the distribution of a species across latitudes.

The North Atlantic Ocean is dominated by the North Equatorial Current to the south and its downstream Gulf Stream system to the north. Ranges of average water temperature along the coastline from south-western England to the Skagerrak were not large either in summer or in winter, ranging from 15.5 to 18 °C in August and from 2 to 7 °C in February (Philippart et al., 1998). This area is dominated by the warm North Atlantic Current, a downstream extension of the Gulf Stream (Sverdrup et al., 1972). The ocean environment along the coastline of northwestern Europe does not differ greatly across latitudes in coastal and offshore waters. Assuming that recruitment variability is basically a function of environmental variation, it is not surprising that no latitudinal differences were found in CVR among stocks of a species in the coastal and offshore waters of northern Europe.

As well as the environmental similarity in waters along the coastline of northwestern Europe, previous studies may have failed to find latitudinal variation because recruitment variations in flatfish are modulated by density-dependent mortality operating primarily at the juvenile stage after fish settle into two-dimensional nursery areas (Van der Veer and Bergman, 1987; Leggett and Frank, 1997). Thus, it may have been difficult to find spatial differences in CVR in such species owing to the presence of density-dependent stabilising processes in the early life stages.

In contrast with the coastline of northwestern Europe, the temperature gradient is steep in the western North Pacific off Japan. The Kuroshio Current (15 °C at a depth of 200 m) and its downstream Kuroshio Extension (Fig. 1) are the western boundary currents of the North Pacific Subtropical Gyre. These currents transport warm and saline waters from the North Equatorial Current, which transports large amounts of heat and materials. Its variability can have considerable effects on climate and fisheries in the western North Pacific. The Oyashio Current (5 °C at 100 m) originates from water outflows from the Sea of Okhotsk and the East Kamchatka Current (Yasuda, 2003), and dominates the north of the western North Pacific. It is a part of the cyclonic circulation of the Western Subarctic Gyre flowing south-westward from the Bering Sea. The Kuroshio Extension and Oyashio Current converge in the Pacific waters off northern Japan. The area between the subarctic Oyashio Front (5 °C at a depth of 100 m; Kawai, 1972) and the

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