Progress in Oceanography 80 (2009) 163–187

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Larval fish abundance and physical forcing in the Gulf of Alaska, 1981–2003

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ARTICLE INFO

Article history:
Received 12 September 2008
Received in revised form 4 March 2009
Accepted 6 March 2009
Available online 17 March 2009

Keywords:
Gulf of Alaska
Fish larvae
Abundance
Physical oceanography
Generalized additive modeling
Early life history

ABSTRACT

The present study investigates ecological patterns and relationships to environmental variables among a time-series of larval fish species abundance from late spring surveys (1981–2003) in the northwest Gulf of Alaska (GOA). Links between interannual variation in species abundance and the physical environment were explored using generalized additive modeling (GAM). Trends in larval abundance and connections with physical variables displayed patterns that indicate unique and complex responses among species to environmental forcing during the larval period. In particular, the observed patterns suggest that ontogenetic-specific responses, representing sub-intervals of early life, are important. In addition, a notable degree of synchrony in larval abundance trends, and similarity in links with physical variables, were observed among species with common early life history patterns. The deepwater spawners, northern lampfish, arrowtooth flounder, and Pacific halibut, were most abundant in the study area during the 1990s, in association with enhanced wind-driven onshore and alongshore transport. Years of high abundance for Pacific cod, walleye pollock, and northern rock sole were associated with cooler winters and enhanced alongshore winds during spring. High larval abundance for spring–summer spawning rockfish species and southern rock sole seemed to be favored by warmer spring temperatures later in the time-series. This apparent exposure–response coupling seems to be connected to both local-scale and basin-scale environmental signals, to varying degrees depending on specific early life history characteristics. Understanding such ecological connections contributes to the evaluation of vulnerability and resilience among GOA species' early life history patterns to fluctuating climate and oceanographic conditions. This investigation also provides crucial information for the identification of "environmental indicators" that may have a broad-spectrum effect on multiple species early life history stages, as well as those that may be more species-specific in exerting control on early life history survival. Of particular interest was the emergence of the EP–NP (East Pacific–North Pacific) teleconnection index as the top-ranked variable in the GAM models exploring the connections between late spring larval abundance and the physical environment. The EP–NP index represents an important and often primary mode of spring–summer atmospheric variability in the northeast Pacific, with a strong expression in the GOA, and its connection with species in this study implies that it may be a climate mode of significant ecological importance.

1. Introduction

The prevailing conceptual view of marine fish recruitment is that of a complex system of interacting biological and physical processes operating at a broad range of spatial and temporal scales (Rothschild, 2000; Hollowed et al., 2001; Bailey et al., 2003, 2005; Ciannelli et al., 2005; Hsieh et al., 2005a). Recruitment is the result of processes operating over several life stages, with a myriad of deterministic and stochastic factors interacting at each stage and across scales to ultimately influence population abundance and variability. Fundamental to understanding complex patterns of recruitment is a detailed knowledge of individual species' biology and life history patterns, and information on prevailing climate and ocean conditions to which each life phase is connected. This is particularly important in the context of the potential impacts of global climate change on fish populations, especially in high latitudes that are experiencing some of the most rapid and severe changes (IPCC, 2007). Knowledge of fish early life history patterns (from the egg stage, through the larval and juvenile phase) and their specific linkages to the marine ecosystem is critical to the development of valid mechanistic models of recruitment prediction. For many marine ecosystems there is a dearth of information on early life history characteristics of their constituent fish populations and their specific connections to prevailing climate and ocean conditions. This inhibits the development of meaningful ecological frameworks for predicting population responses to environmental change. Such predictive models need to incorporate

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0079-6611/$ - see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.pocean.2009.03.002

species-specific patterns of exposure to the environment prior to recruitment.

Several decades of fisheries science and oceanographic studies in the Gulf of Alaska (GOA), especially by the Ecosystems and Fisheries Oceanography Coordinated Investigations (EcoFOCI) Program at the National Oceanic and Atmospheric Administration's (NOAA) Alaska Fisheries Science Center in Seattle, WA, USA, has produced an extensive body of knowledge of this ecosystem, including physical and biological (lower trophic level) processes as well as life history patterns of the diverse range of resident fish populations (Napp et al., 1996; Coyle and Pinchuk, 2003; Matarese et al., 2003; Doyle et al., 1995, 2002; Stabeno et al., 2004; Bailey et al., 2005; and others). Fluctuations in biomass of major commercial and ecologically important groundfish species, including walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), sablefish (*Anoplopoma fimbria*), and a variety of flatfish species (Pleuronectidae), as well as certain small forage species such as capelin (*Mallotus villosus*), herring (*Clupea harengus*) and greenlings (Hexagrammidae), have been documented over the past four decades in the GOA. Many studies have suggested associations between production of these species and certain patterns of climate change, particularly the major shift in the late 1970s (termed a climate regime shift) from relatively cool to relatively warm ocean conditions (Anderson and Piatt, 1999; Hare and Mantua, 2000; Hollowed et al., 2001; Ciannelli et al., 2005; Litzow, 2006; Mueter et al., 2007). Despite the observed patterns in fish production and the ocean environment in the GOA, reliable predictions of recruitment strength remain elusive for most species. For certain species, such as walleye pollock, we have some understanding of mechanisms of environmental forcing during the earliest life history phase and their impact on the general patterns of recruitment (Bailey et al., 2005). However, much can still be gained from ongoing studies in this region. In particular, investigating relationships between the early life history dynamics of fish species and their ocean and climate environment is likely to contribute significantly to our understanding of the impact of changing ocean conditions on recruitment processes in the GOA.

The present study investigates a 21-year time-series of abundance of numerically dominant larval fish species from 1981 to 2003 (there was no sampling in 1984 and 1986) in the northwest GOA. The main objective of the ichthyoplankton surveys during this period was the investigation of factors affecting the recruitment of the population of walleye pollock that spawns in Shelikof Strait, GOA, during late winter to early spring. The late spring collections were timed and located primarily to coincide with the occurrence of late-stage walleye pollock larvae in the plankton of shelf and adjacent deep waters in and downstream from Shelikof Strait (Kendall et al., 1996). This mid-May to early June time-series of ichthyoplankton data also yields significant information on the early life history stages of other winter and spring spawning fish species in the GOA. During spring, larval abundance is at a peak for most GOA fish populations (Matarese et al., 2003), and larval fish species diversity is highest in the vicinity of Shelikof Strait, indicating the importance of these coastal and shelf waters as spawning and hatching areas for local fish populations (Doyle et al., 2002). In combination with basin- and local-scale measures of the state of the atmosphere and ocean during these years, these ichthyoplankton data offer an important opportunity to explore multispecies links between fish early life history and the physical environment in the GOA.

Our principal objectives in this study were to document interannual patterns of variation in the abundance of the numerically dominant larval fish species in the GOA during late spring, and to investigate relationships between the larval abundance patterns and physical oceanographic and climate variables. In addition, we identify among-species synchronicity in the larval abundance time-series, and similarities in the species to physical variable connections. Links between the species abundance and the physical variables are interpreted from the perspective of fish life history strategies and potential mechanisms of physical forcing on early life history aspects of recruitment processes in the GOA ecosystem.

2. Methods

2.1. Study area

The bottom topography of the western GOA is complex. It is characterized by a relatively narrow continental shelf (65–175 km wide) punctuated by many deep canyons, shallow banks, and numerous bays and inlets intersecting the coast. Along the shelf edge the continental slope drops abruptly to depths of 5000–6000 m (Fig. 1). The regional meteorology is dominated by strong cyclonic winds that blow from fall through spring, and by strong storms that vary on monthly to decadal scales (Stabeno et al., 2004). Substantial freshwater runoff occurs from late spring through fall, and with the winds drives the coastal circulation along the Alaska Peninsula. Two current systems dominate the circulation in the western GOA, the Alaskan Stream (the western boundary current of the eastern sub-arctic gyre) along the margin of the ocean basin and the Alaska Coastal Current (ACC), a vigorous coastal current with a seasonally variable freshwater core, on the continental shelf (Stabeno et al., 2004) (Fig. 1). The Alaskan Stream flows southwesterly and roughly parallel to the shelf break at >50 cm s^{-1} near the surface. Nearshore, the upper layer of the ACC flows southwesterly, and in the vicinity of Shelikof Strait the ACC is one of the most vigorous and dynamic coastal currents in the world (Stabeno et al., 1995). In response to variations in wind forcing and freshwater input, maxima in alongshore transport can exceed $3.0 \times 10^6\ m^3\ s^{-1}$ and daily averaged speeds can exceed 100 cm s^{-1} (Stabeno et al., 2004). At the northeast entrance to Shelikof Strait, the ACC bifurcates around Kodiak Island with the majority of the annual transport continuing down the Strait. The ACC is a primary path of dispersal for many planktonic organisms including fish eggs and larvae. Circulation features such as eddies, and deep advection in canyons, also influence the influx and retention of plankton organisms on the shelf as well as the supply of nutrients from deeper water (Napp et al., 1996; Stabeno et al., 2004).

Water temperatures follow a clear seasonal pattern, with the coldest values occurring in March and the warmest values in August (Reed and Schumacher, 1986; Stabeno et al., 2004). A seasonal peak in phytoplankton production occurs first in the ACC, and then in the adjacent shelf area, during early May, and production of copepod nauplii and other zooplankton usually accelerates significantly at this time (Cooney, 1986; Napp et al., 1996; Coyle and Pinchuk, 2003). The zooplankton production season on the GOA shelf extends from March to October with copepod dominated biomass and abundance peaks occurring in May and July, respectively (Incze et al., 1997; Coyle and Pinchuk, 2003). Seasons are defined in this study by solstice and equinox intervals: winter extends from December 22nd to March 21st, spring from March 22nd to June 21st, summer from June 22nd to September 21st, and autumn from September 22nd to December 21st.

2.2. Ichthyoplankton data

Ichthyoplankton data were collected during spring surveys conducted by the Recruitment Processes Program at the Alaska Fisheries Science Center (AFSC), from 1981 to 2003 (Matarese et al., 2003). For these years ichthyoplankton sampling was most intense