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Transport patterns of Pacific sardine *Sardinops sagax* eggs and larvae in the California Current System

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ABSTRACT

We simulated transport of Pacific sardine eggs captured offshore of California in spring of 2001–2012 using a regional ocean circulation model. Eggs were assumed to have developed into larvae within a few days and were modeled using five behavioral patterns: passive transport, diel vertical migration, diel vertical migration combined with swimming against the current, diel migration combined with migration toward shore, and diel migration combined with migration toward the best habitat. Simulated larvae with no swimming behavior were advected far offshore to poor habitat where they were unlikely to survive. Diel vertical migration resulted in less offshore transport because larvae were less affected by surface currents during the day. However, in half the years simulated nearly all juveniles were also located in poor habitat by late summer in this scenario. Swimming against the current combined with diel vertical migration resulted in similar transport patterns to the diel-vertical-migration scenario because currents dominated the transport of eggs and small larvae during the spring and early summer. Migration toward shore resulted in a large fraction of juveniles being located in appropriate habitat during late summer in all years. Migration toward the best habitat was the best strategy modeled. This strategy resulted in a slightly greater proportion of larvae being located in appropriate habitat at the end of summer than the swimming-toward-shore scenario, despite the fact that most larvae were located farther offshore. These results suggest that larval sardine might use directed horizontal swimming behavior to remain in suitable habitat conditions. A large fraction of larvae were transported south into Mexican waters by late summer in all five scenarios. Surveying juvenile sardines in fall near the border of the U.S. and Mexico may be an efficient means of estimating recruitment because the advection pattern of eggs and larvae to the south is opposite the adult migration pattern to the north. This pattern may cause juveniles to be spatially segregated from adults at the time they are being recruited.

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1. Introduction

The Pacific sardine *Sardinops sagax* is a coastal pelagic species that occurs in the California Current offshore of western North America from the tip of Baja California to the Gulf of Alaska, and in the Gulf of California. It forms an important trophic link between zooplankton and larger avian, fish, and mammalian predators when populations are sufficiently large (e.g., Chen et al., 2009). However, the abundance of Pacific sardines fluctuates greatly through time. The fishery for Pacific sardine was the largest single-species fishery in the world during the 1930s but collapsed as sardine abundance declined precipitously in the late 1940s (Radovich, 1982). The fishery resumed in the U.S. and Canada during the 1990s following a population recovery but has shown signs of declining again in recent years (Hill et al., 2014). Such fluctuations have occurred for thousands of years even in the absence of fishing (Baumgartner et al., 1992). They appear to be the result of environmental variability (Lluch-Belda et al., 1992), although fishing may also interact with the environment to control stock size (Zwolinski and Demer, 2012). As with most pelagic marine species, survival rates of sardine larvae and juveniles are relatively low but exhibit great interannual variability. The proportion of juvenile sardines that survive this period, i.e., the rate of recruitment, is the most important determinant of population size (Clark and Marr, 1955; Murphy, 1967).

Transport patterns of eggs and larvae have large effects on subsequent recruitment of pelagic fishes because eggs must be

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released into appropriate habitat and then retained, or drift toward, appropriate nursery habitat to survive (Bakun, 1996). The habitat must have appropriate physical conditions (e.g., temperature and salinity), sufficient prey, and relatively few predators. Pelagic fishes generally are adapted to take advantage of typical annual flow patterns (Norcross and Shaw, 1984). However, identical transport patterns may result in exposure to different environmental conditions among years because oceanic environmental conditions are also dynamic. Conditions that eggs and larvae encounter are the product of the geographic area in which adults congregate for spawning, movement of eggs and larvae by advection, swimming behavior of larvae, and dynamics of environmental conditions during the spawning and rearing period.

Modeling transport patterns and environmental conditions to which larvae are exposed by entering them as passive or active particles in hydrodynamic models is an appealing method of examining their early life history because this approach can provide insight into population level effects of environmental conditions (Werner et al., 1997). The approach also provides a testable framework for explaining the effects of environmental variability on fish populations. Coupled biophysical models that provide estimates of primary and secondary production along with estimates of physical properties from a circulation model show particular promise in explaining fish population dynamics (e.g., Machu et al., 2009; Kishi et al., 2011; Xu et al., 2013). However, the sensitivity of predictions from coupled physical-biological models of fish recruitment to their underlying physical and biological parameterization has seldom been tested. Where supporting empirical data are scarce, it is difficult to evaluate how closely model simulations represent reality. An important application of coupled physical-biological models that has been used less frequently, but is particularly appropriate where data are scarce, is to develop likely scenarios that can be tested with empirical observations (Miller, 2007).

Accurately modeling larvae and small juvenile sardine in the California Current is difficult because their movement patterns, environmental preferences, and population vital rates have not been well documented. Although eggs and smaller larvae of sardines have been well sampled in the California Current as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI; cf., McClatchie, 2014) and Investigaciones Mexicanas de la Corriente de California programs (cf., Baumgartner et al., 2008), larger larvae and juveniles are captured rarely. This is because most of the research sampling conducted has been directed toward capturing ichthyoplankton using bongo nets (cf., Smith and Richardson, 1977) or similar gear. Larvae typically develop limited ability to avoid these nets within less than one week after hatching and are captured rarely in bongo nets after about 45 days (24 mm in length; Ahlstrom, 1954; Lo et al., 1989, 1996). Pacific sardine generally are not sampled again until they are captured as adults in the fishery.

The population of Pacific sardine includes three subpopulations that are not genetically distinct (Hedgecock et al., 1989) but exhibit separate spawning aggregations (Ahlstrom, 1954; Smith, 2005). One subpopulation occurs in the Gulf of California. The other two are known as the northern subpopulation and the southern subpopulation. The northern subpopulation ranges from northern Baja California to southeastern Alaska. The southern subpopulation ranges from the tip of Baja California to southern California. Although the ranges of the northern and southern subpopulations overlap, adults from both populations migrate in synchrony to the north in late spring and summer, and to the south in late fall and winter. There is evidence that habitat preferences differ between the sub-populations (Demer and Zwolinski, 2014). Thus, their geographical overlap is believed to be minimal.

Adult sardines of the northern subpopulation congregate to spawn offshore of central or southern California during the late winter and spring. Specific spawning locations within the broad area are strongly affected by oceanographic conditions (e.g., Checkley et al., 2000; Weber and McClatchie, 2010; Zwolinski et al., 2011). Although little is known about the subsequent movements of larvae, a few studies have reported that larger Pacific sardine larvae congregate offshore of Baja California (Scofield, 1934; Ahlstrom, 1954). These results suggest that larvae may be actively swimming toward shore because the prevailing currents move offshore to the southwest (Scofield, 1934).

The Continuous Underway Fish Egg Sampler (CUFES; Checkley et al., 1997, 2000) collects pelagic eggs through a pump in the ship's hull. Sardine eggs are positively buoyant and typically accumulate near the surface after spawning (Curtis et al., 2007). Their vertical distribution is affected by seawater density but generally the greatest portion of the distribution occurs in the upper 20 m. Because sardine eggs develop into larvae within a few days, the CUFES is used to survey potential sardine habitat during the spawning period to provide a synoptic estimate of the spawning habitat that has been used (Lo et al., 2011; Zwolinski et al., 2011).

The spawning habitat of the northern subpopulation of Pacific sardines, as determined by egg distributions, has been modeled with relatively good accuracy using data from the CUFES (Checkley et al., 2000; Reiss et al., 2008; Zwolinski et al., 2011; Nieto et al., 2014) and bongo nets (Weber and McClatchie, 2010). These previously published statistical models indicate that sea-surface temperature and chlorophyll concentration (a proxy for production of prey items) are the strongest predictors of appropriate habitat. Sea surface height (Asch and Checkley, 2013), sea surface height gradient, and salinity also provide explanatory power. Zwolinski et al. (2011) reported that despite their long migrations along the U.S. west coast, adult sardine use the same habitat in terms of sea-surface temperature, chlorophyll concentration, and geostrophic flow throughout the year that they do during spawning (as opposed to fishes like salmon that switch to very different environments). If larval and juvenile sardine use similar habitat to adults and eggs, a habitat model based on environmental conditions at spawning may be used as a convenient univariate index of habitat conditions experienced by larvae as they develop (i.e., areas with greater predicted probability of capturing eggs are considered to have greater habitat quality). Tracking simulated sardine larvae in a coupled biophysical model over this period is a promising approach to understanding their behavior and recruitment because such biophysical models produce estimates of the variables needed to predict habitat quality.

We simulated transport of sardine eggs and larvae in a hydrodynamic model for several swimming behaviors using the positions of eggs captured in the CUFES during the spawning season as starting points. For each simulation, we used environmental characteristics estimated by the hydrodynamic model and coupled biophysical model to evaluate the quality of the habitat encountered by simulated larvae. The objective of the study was to test the effects of swimming behavior on transport patterns and environmental conditions encountered, and thereby quantify likely transport patterns for Pacific sardines of the northern subpopulation (hereafter referred to as sardine) from the egg stage to the juvenile stage at the end of summer.

2. Material and methods

Sardine eggs were collected using the CUFES during spring cruises offshore of California from 2001 through 2012 (Fig. 1). The CUFES collected eggs through a pump on the ships hull at a depth