Testing early life connectivity supplying a marine fishery around the Falkland Islands

Julian R. Ashford [a,*], Bettina A. Fach [b], Alexander I. Arkhipkin [c], Cynthia M. Jones [a]

[a] Center for Quantitative Fisheries Ecology, Old Dominion University, 800 West 46th St., Norfolk, VA 23529, USA
[b] Institute of Marine Sciences, Middle East Technical University, PO Box 28, 33731 Erdemli, Turkey
[c] Fisheries Department, Falkland Islands Government, Stanley, Falkland Islands

ABSTRACT

We used a wind-driven global circulation model to build spatially explicit predictions from rival hypotheses concerning advective supply of Patagonian toothfish (*Dissostichus eleginoides*) to a trawl fishery around the Falkland Islands, and tested the predictions using chemistry recorded in the otoliths of fish caught in the fishery. Model simulations indicated transport pathways from spawning aggregations off southern Chile to both the north and south of the fishing area. In contrast, simulated particles released from spawning aggregations around Burdwood Bank were transported to the south of the fishing area but not to the north, becoming fully entrained in the Subantarctic Front instead. Spatial heterogeneity in the chemistry laid down in the otolith nuclei during early life discounted the hypothesis of a single population with a spawning area on Burdwood Bank, and indicated that fish assemblages are structured by large-scale transport from both southern Chile and Burdwood Bank. By linking fish explicitly to their physical environment, the two techniques can help distinguish the life cycle trajectories necessary for populations to persist, and elucidate the interactions between hydrography and life history that structure the fish assemblages on which marine fisheries depend.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

1.1. Competing life history hypotheses

Many marine fisheries target fish stocks that are structured by their physical environment; as a result, the spatial relationships between physical and biological processes are potentially key to understanding their distribution and abundance. In populations that are geographically contained by barriers like oceanic fronts or deep water (e.g. Kingsford, 1993; Loeb et al., 1993), the dynamics are defined by births and deaths of inter-breeding fish isolated within discrete domains that can be managed independently, and the life-cycle is closed through local retention and self-recruitment (e.g. Almany et al., 2007). However, dispersal and movement can connect geographically distant areas, giving coherence to life history cycles in which life stages take advantage of different habitats (e.g. Harden Jones, 1968; Cushing, 1981; Thorrold et al., 2001). Moreover, immigration from outside sources can subsidize populations in which low self-recruitment relative to mortality otherwise leads to extinction (Pulliam, 1988). Since dispersal often occurs during early life before active movement is well developed, the large-scale circulation can strongly influence the direction and extent of connections between habitats and populations, and hence the spatial composition of the fish assemblages which fisheries harvest.

Around the Falkland Islands off south-eastern South America, a longline fishery harvests adult Patagonian toothfish (*Dissostichus eleginoides*) along the continental slope (e.g. Laptikhovsky et al., 2006). Greater numbers, however, are caught as juveniles in a trawl fishery in the Falkland Islands Interim Conservation and Management Zone (FICZ) on the Patagonian Shelf (Laptikhovsky and Brickle, 2005). Evidence from genetics (Shaw et al., 2004; Rogers et al., 2006) indicates that toothfish off South America are separated from those in the Antarctic, by a population boundary in the vicinity of the Polar Front in the Antarctic Circumpolar Current (ACC) (Fig. 1). Equatorward of the Polar Front, spawning adults have historically been found only in an area on the Burdwood Bank and western North Scotia Ridge, suggesting that fisheries around the Falkland Islands are supplied by a single discrete population (Laptikhovsky et al., 2006).

Toothfish are slow-growing and live to 50+ years (Ashford, 2001; Horn, 2002). Exceptionally fecund for notothenioids, the females produce up to 250,000 large eggs of ca. 1 mm diameter during spawning (e.g. Nevinski and Kozlov, 2002). The eggs and larvae are pelagic (Evseenko et al., 1995; North, 2002): egg develop-

* Corresponding author. Tel.: +1 757 683 4804; fax: +1 757 683 5293.
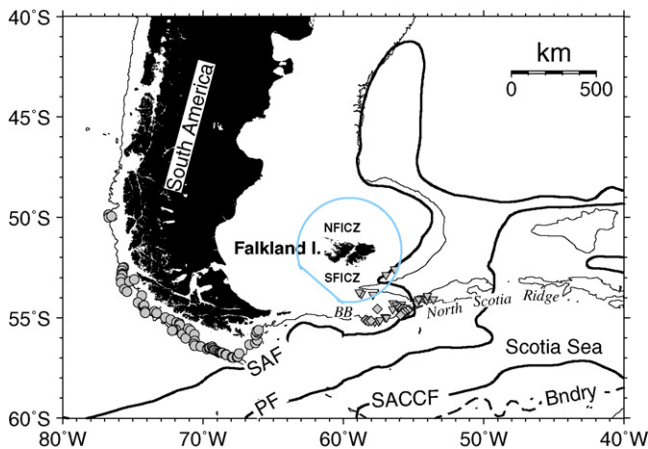*E-mail address:* jashford@odu.edu (J.R. Ashford).

Fig. 1. Study area. Grey circle shows boundary of Falkland Islands Interim Conservation and Management Zone (FICZ). Continuous dark lines mark the mean position of major fronts: SAF, Subantarctic Front; PF, Polar Front; SACCF, Southern Antarctic Circumpolar Current Front; Bndry, southern boundary of the ACC (shown as a dashed line). All fronts after Orsi et al. (1995). Thin lines mark the 2000 m isobar. Abbreviations: BB—Burdwood Bank; NFICZ—North FICZ; SFICZ—South FICZ. Symbols mark drifter release sites corresponding to observed spawning locations off southern Chile (●), and Burdwood Bank of first (▲) and second (♦) peak spawning sites after Laptikhovsky et al. (2006). Scale bar shows distance at 45° S.

ment lasts up to ca. 90 days (Evseenko et al., 1995) and the larval period spans ca. 230 days (Krusic-Golub et al., 2005). In contrast, juvenile toothfish are negatively buoyant (Eastman, 1993) and move demersally in shelf habitats on scales of only ca. 25 km (Williams et al., 2002). Ontogenetic movement to adult feeding grounds in deeper water along continental slopes (e.g. Agnew et al., 1999) is associated with a change to neutral buoyancy around maturity (Eastman, 1993), which considerably reduces the energy needed to move using currents in the ACC (Ashford et al., 2005). As a result, toothfish life history is marked by important ontogenetic changes in the spatial scales of movement, with the potential for connectivity on scales of 1000s of kilometres through advection of young stages, and also adults.

Circumpolar flow in the Southern Ocean, concentrated in jets associated with the frontal systems in the ACC (e.g. Orsi et al., 1995), passes through a constriction between South America and the Antarctic Peninsula in the Drake Passage. Equatorward of the Polar Front, the Subantarctic Front (SAF) passes south of Cape Horn and Burdwood Bank and north through a trough 2000 m deep in the North Scotia Ridge, to align subsequently with the 2000 m isobath along the Patagonian Shelf slope (Fig. 1) (Arhan et al., 2002). After spawning during May–July, spent female toothfish are found along the slope south of the Falkland Islands (Laptikhovsky et al., 2006), consistent with advection from the Burdwood Bank along the SAF to feeding areas downstream (Ashford et al., 2007). Moreover, larvae found north of the Burdwood Bank during December (North, 2002), 100–200 days after spawning, suggest a connection via advection to juvenile areas exploited by the trawl fishery in the FICZ.

A single discrete population recruiting from the spawning aggregation around Burdwood Bank implies that all fish on the Patagonian Shelf share a common early life history. However, while evidence from otolith chemistry successfully confirmed the population boundary in the vicinity of the Polar Front, it also suggested mixing along the Patagonian Shelf slope between two South American source populations (Ashford et al., 2006). Researchers have recently found a second area with fish spawning in June–July near the SAF but upstream of Burdwood Bank along the south-west shelf-slope off Cape Horn in the Chilean Exclusive Economic Zone (Arana, 2009). If young stages spawned there as well as the Burd-

wood Bank supply the FICZ, changes in the position and intensity of the SAF, and in spawner abundances at considerable distances from the Falkland Islands, may directly impact local recruitment and subsequent catches in the trawl fishery.

1.2. Testing using a spatially explicit approach

Mounting evidence that fish otoliths record hydrographic exposures (e.g. Bath Martin and Thorrold, 2005; Walther and Thorrold, 2006), combined with the chronology delineated in growth increments, makes otolith chemistry a particularly powerful technique for testing population hypotheses that involve a strong physical component. Previous studies of Patagonian toothfish indicated that the concentration of $MgCa^{-1}$ laid down in the otolith was related to spatial differences in fish activity, most likely in response to fast-moving currents and eddies. Otolith $MnCa^{-1}$, on the other hand, appeared related to resuspension or authigenic activity on the Patagonian Shelf, whereas $SrCa^{-1}$ distinguished growth mediated by temperatures characteristic of different water masses, and $BaCa^{-1}$ reflected ambient concentrations of dissolved Ba associated with nitrate-fueled production in open water (Ashford et al., 2005). Based on concentrations of these markers, toothfish caught along the Patagonian Shelf re-assigned to region with 94–95% accuracy (Ashford et al., 2005, 2007), and between areas separated at scales of 100s of kilometers along the shelf with a success rate of between 57 and 83% (Ashford et al., 2007).

Exposure to hydrographic properties characteristic of water masses and circulation therefore leaves a record that fish carry with them, which can be used retrospectively to detect connectivity and examine the spatial composition of harvested fish. Despite these physically based response variables, however, fisheries researchers have to date rarely tested hypotheses that incorporate an explicit oceanographic context. Typically, tests are between a null hypothesis of spatial homogeneity in the chemistry laid down in the otolith nuclei, consistent with a common early life history, and an alternative hypothesis of heterogeneity indicative of geographically discrete populations. But fish from several populations mixing in different proportions can also generate spatially heterogeneous distributions, and the approach gives little insight into the complex physical–biological interactions that can underly the population dynamics supporting fishing activity.

A more spatially sensitive approach that incorporates the large-scale circulation is to test hypotheses using particle simulations (e.g. Fach and Klinck, 2006; Thorpe et al., 2007). Inputs and assumptions are rigorously specified but nonetheless, the uncertainties involved in reproducing physical processes often undermine conclusions from these tests. Combined with otolith chemistry, however, particle simulations provide a quantitative means of constructing spatially explicit hypotheses that incorporate the physical circulation, with well-defined predictions of expected trajectories that can be empirically tested against observed distributions in the otolith chemistry (Ashford et al., 2010, 2011b).

In this study therefore, we simulated pelagic transport pathways along the SAF to build spatially explicit predictions that distinguished the rival hypotheses of a single discrete toothfish population versus mixing between fish from two populations, using easily accessible and widely used current velocity fields taken from the OCCAM global circulation model (Webb et al., 1998; Saunders et al., 1999; Webb and de Cuevas, 2003). We used chemistry recorded in the otolith nuclei of toothfish caught in the fishery to test between the predictions, following methodology now well established in the literature (e.g. Dorval et al., 2005; Ashford et al., 2011a). We also measured the chemistry along the otolith edges to examine empirically how recently laid down material varies spatially within the FICZ.