Spawning site fidelity and fine-scale population structuring of Atlantic cod in the Gulf of Maine

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Introduction:

The Gulf of Maine stock of Atlantic cod is currently overfished and overfishing is occurring (NEFSC 2012). Concurrent with declines in abundance in recent decades have been reductions in biocomplexity (Alexander et al. 2009), most notably decreases in spawning diversity (Ames 2004). Atlantic cod populations have been suggested to demonstrate metapopulation structuring where individual spawning components function as subpopulations (Rose et al. 2011; Smedbol and Wroblewski 2002; Wright et al. 2006a). These subpopulations are often genetically-isolated (Kovach et al. 2010; Pampoulie et al. 2006; Ruzzante et al. 1998), and they can form in the absence of physical barriers or great distances (Knutsen et al. 2003). Potential mechanisms influencing fine-scale population structuring include restricted dispersal at early life stages (Byers and Pringle 2006; Churchill et al. 2011; Espeland et al. 2007), temporal variation in spawning (Kovach et al. 2010; Ruzzante et al. 1998), differences in spawning habitat (Grabowski et al. 2011), spawning site fidelity (Green and Wroblewski 2000; Robichaud and Rose 2001; Skjaeraasen et al. 2011; Wright et al. 2006b), and natal homing (Svedang et al. 2007). This written summary will focus on the expression of spawning site fidelity by Atlantic cod and the associated fine-scale population structuring of cod in the Gulf of Maine region. Key papers related to the topics will be reviewed and a synthesis of cod stock structure including future research needs are included.

Summary of Key Papers:

Stephenson, R.L. 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. Fisheries Research 43, 247 - 249.

According to Stephenson (1999), there has been increasing interest in stock identification at smaller scales than have been considered previously. Common assessment techniques and management strategies assume discrete populations, but management units typically contain stock complexes or metapopulations with several spawning components rather than consisting of a single discrete population. The importance of individual spawning groups to assessment and management has received little attention as fisheries have been managed in units which are based on a combination of biological, political, and administrative boundaries. Many spawning areas have been lost at least partly due to the management of fisheries using simple population units that do not always match biological population structure. Consequently, there has been relatively little consideration for the degree of discreteness or the ecological significance of spawning components. Stephenson (1999) argued that sub-units of a population should be treated as discrete, and conserved. Further, the persistence of the full diversity of spawning stocks within each management unit should become a priority of management.

Ames, E.P. 2004. Atlantic cod stock structure in the Gulf of Maine. Fisheries 29(1), 10-28.

In order to tentatively identify subpopulations and spawning components of Atlantic cod in the Gulf of Maine, Ames (2004) evaluated the distribution and dynamics of cod using 1920's data and surveys from retired fishermen. The distribution and spawning areas of the historic spawning components were compared to modern tagging studies and egg distribution surveys. Cod were speculated to migrate seasonally and return to the same spawning areas annually. Four subdivisions with discrete migration corridors, local cyclical movements to and from the spawning grounds and nursery areas, and partial isolation due to bathymetry were identified. Each subdivision was composed of clusters of spawning components, or local stocks that functioned as subpopulations. The presence of continued spawning activity by some historic spawning components was confirmed with modern egg surveys. However, approximately half of the historic spawning components appear to be extinct, resulting in reductions of reproductive capacity which have coincided with gradual, long-term depletion. The spawning components were speculated to have collapsed in response to increased fishing effort in coastal waters, pollution of coastal nursery grounds, and the destruction of anadromous forage stocks. System-wide assessments were believed to be unable to detect the gradual erosion of spawning components. The geographical character of subpopulations and spawning components was suggested to be a pivotal factor in rebuilding and maintaining Gulf of Maine cod and it was suggested that subpopulations are the appropriate management unit to minimize further losses of spawning components while rebuilding the fishery.

Robichaud, D. and Rose, G.A. 2001. Multiyear homing of Atlantic cod to a spawning ground. Canadian Journal of Fisheries and Aquatic Sciences 58, 2325-2329.

Robichaud and Rose (2001) sought to determine the degree of multiyear fidelity of cod to a major spawning ground in Newfoundland waters. A total of 48 cod were tagged with acoustic transmitters during April 1998. Fish were monitored during the spring spawning season of 1998, 1999, and 2000 using active tracking. Homing rates were calculated as the proportion of tagged fish that returned to Bar Haven during the spawning season. Rates were adjusted based upon relocation efficiency (80%), transmitter failure rate (6%), natural mortality (20%), tag-induced mortality (6%), and fishing mortality. All fish that were relocated in subsequent spawning seasons were within 10km of the Bar Haven spawning site where they were released, with the majority being within a few hundred meters. The fate of non-relocated fish remains uncertain; however, none were observed on other known spawning grounds. Homing rates adjusted for mortality, under-reporting, and tag failure for the 1999 and 2000 spawning seasons were 39% and 54%, respectively. Multiyear homing to the Bar Haven spawning site was observed in 26% of cod. Unaccounted for transmitters during the spawning season implies that straying did occur, and potential genetic exchange among adjacent populations might have resulted. Newfoundland cod fisheries are managed over spatial scales far exceeding those of the stock structure suggested by their results. The authors believe that cod have achieved a life-history balance between homing and straying that maintains population stability, while also permitting recolonization of inactive spawning sites. However, the accurate and prevalent homing behavior observed in this study would impede quick recolonization.

Skjaeraasen, J.E., Meager, J.J., Karlsen, O., Hutchings, J.A., and Ferno, A. 2011. Extreme spawning-site fidelity in Atlantic cod. ICES Journal of Marine Science 68(7), 1472-1477.

To investigate the smallest spatial scales at which population dynamics processes and adaptation arise in Atlantic cod, Skjaeraasen et al. (2011) studied the movements and homing behavior of individual cod at a small coastal spawning site off Newfoundland. In late February 2007, a total of 40 cod were released with individually coded ultrasonic tags to track them on the spawning site. The cod were recorded on the spawning ground for several months during the spawning season the following winter from December 2007 through March 2008. Not a single transmitter was detected on the spawning ground outside of the spawning season (June 2008 through November 2008), suggesting that the area functions mainly as a spawning ground. Minima of 55% and 37% of the tagged fish still at liberty were present on the spawning ground in 2008 and 2009, respectively. These findings are consistent with the hypothesis that cod exhibit homing and fidelity to their spawning grounds, and their results are suggested to be the first to demonstrate spawning site fidelity on such a small geographic scale (<1 km). In fact, the actual proportion of tagged fish on the spawning ground was likely higher since no corrections for factors such as reporting rate or natural mortality were accounted for. Not all the tagged cod were observed at the spawning ground, suggesting some degree of infidelity, or cod spawning at other sites in subsequent years. Such a high rate of philopatry provides the necessary condition for the evolution of local adaptation. Their results identified the potential for genetic differentiation and population structure on a spatial scale considerably finer than that suggested previously for cod.

Siceloff, L. and Howell, H. In Press. Fine-scale temporal and spatial distributions of Atlantic cod (Gadus morhua) on a western Gulf of Maine spawning ground. Fisheries Research. http://dx.doi.org/10.1016/j.fishres.2012.04.001

Siceloff and Howell (2012) sought to describe the seasonal migration of Atlantic cod in Ipswich Bay to examine their spawning behavior, spatial distribution, and habitat utilization during the spawning period. Acoustic telemetry and archival data storage tags (DSTs) were used to collect fine-scale movement data. In 2006, a total of 200 spawning cod were tagged with DST's, with 26 of these fish also tagged with an acoustic transmitter. Acoustically tagged fish were monitored on the spawning site using both moored acoustic receivers and active tracking from May 6 - June 30. Acoustic telemetry data was analyzed by constructing minimum convex polygons (MCPs) and kernal distribution estimates (KDEs) to illustrate the cod's spatial distribution and to identify centers of activity. Volume contours enclosing 95% of each cod's utilization distribution were derived from the KDEs to characterize each cod's area of primary activity. Most cod aggregated around a large bathymetric feature known as "Whaleback", with most activity occurring on the east and west ends. The MCP derived from all pooled manual tracking data was approximately 60 km^2. Individual volume contours overlapped in an area encompassing ~100 km^2, stretching ~12km from east to west. Individuals were typically active in areas ranging from approximately 17 - 57 km^2, with a mean area of 41 km^2. Movements were characterized by group shifts between the east and west ends of Whaleback from May 17 - June 15 until most cod departed. Data collected from recovered DSTs showed concurrence between last detections from acoustic telemetry and deep-water shifts in DST records. Tracking data demonstrated that spawning cod aggregated around a specific group of raised bathymetric features, that cod spawn predictably alongside vertical relief and around specific sites, utilize relatively small areas during spawning, are highly mobile within those areas, and tend to move as a group. Their results demonstrate the relatively fine-scales at which spawning occurs in the Gulf of Maine, which may serve as an isolation mechanism between separate spawning components.

Zemeckis, D., Hoffman, W., Dean, M., Armstrong, M.P., Martins, D., and Cadrin, S.X. In progress. Movements of spawning cod in the western Gulf of Maine.

Zemeckis et al. (In progress) utilized acoustic telemetry to investigate the movements of spawning cod in the western Gulf of Maine. Acoustic transmitters were released in the Spring Cod Conservation Zone (SCCZ), a seasonal closure designed to protect spawning cod in Massachusetts Bay. A total of seven cod were tagged with acoustic transmitters in 2009, with 52 cod being tagged in 2010 and four cod being tagged in 2011. A Vemco Positioning System (VPS) was deployed to monitor cod movements in the SCCZ during the spawning season from 2009 through 2012. Telemetry data was examined for the expression of spawning site fidelity and residence times on the spawning site were calculated. Fine-scale (<100 m), multi-year spawning site fidelity was documented in the SCCZ. Three of the seven cod tagged in 2009 returned to the SCCZ in 2010. Two of these fish also returned in 2011, with one also being detected in 2012. A total of 15 of the 52 cod released in 2010 returned to the SCCZ in 2011. Multiyear spawning site fidelity has also been documented for cod tagged in 2010. Investigation of the 2011 telemetry data yields adjusted rates of spawning site fidelity of >70% when natural mortality and fishing mortality are accounted for. Residence times of cod ranged from 4 -106 days, with a mean of 36 days. The expression of spawning site fidelity within this spawning component confers complex population structuring within Gulf of Maine cod. However, rates of spawning site fidelity <100% suggest 'infidelity' where tagged cod are visiting different spawning sites in subsequent seasons. Fishery recaptures provides evidence of such infidelity. Additional evidence of connectivity among coastal spawning sites has been collected in 2012 acoustic telemetry data, fishery recaptures of tagged cod, and sea-sampling of commercial catch. Despite evidence of infidelity and connectivity among spawning sites, the high rates of spawning site fidelity observed corroborate results of previous work by confirming that rates of recolonization of inactive spawning sites are likely to be low.

Synthesis of Stock Structure:

The erosion of spawning components and the existence of fine-scale population structuring within cod stocks has been well demonstrated (Ames 2004; Stephenson 1999). The expression of spawning site fidelity (Zemeckis et al., In progress) and fine-scale spawning activity in the Gulf of Maine (Siceloff and Howell 2012) confer complex population structuring within the stock. Failure of management strategies to account for this complex stock structure is expected to lead to continued declines in diversity (Stephenson 1999), which can go undetected by system-wide assessments (Ames 2004). This is significant because reductions in spawning diversity are expected to increase the risk of widespread recruitment failure (Begg and Marteinsdottir 2000; Sinclair 1988) and reduce stock productivity and stability (Kerr et al. 2010). Therefore, it is crucial that management plans address fish complexes at the appropriate scales to preserve stock complexity and rebuild collapsed stocks (Stephenson 1999). Treating complex structuring of cod populations such as that observed in the Gulf of Maine as a single stock is expected to result in biased estimates of spawning stock biomass, annual yield, and recruitment, while simultaneously masking steady declines in these variables as spawning aggregations become depleted (Reich and DeAlteris 2009). In order to be effective, management strategies must acknowledge the complex population structure of cod (Kovach et al. 2010) to better account for natural biological processes. To promote recovery of a depleted population, a key factor is to identify the spawning areas which act as the main source of settling pelagic juveniles and act to protect these areas, as well as limit fishing in the target area (Heath et al. 2008).

Future management plans should address the recolonization of inactive spawning sites. Unproductive spawning sites might be naturally restored to their previous levels of productivity by the resurgence of a remnant population or by recolonization of cod from other spawning sites (Wroblewski et al. 2005). Future research efforts should focus on gaining a better understanding of the movements and connectivity between individual spawning components to evaluate potential mechanisms for recolonization. Future research should also focus on improving our understanding of the fine-scale spawning behavior of cod. Improved understanding of cod spawning dynamics would help to identify reproductive isolation mechanisms and help to investigate fine-scale population structuring, including how individual spawning components differ and how genetically distinct and reproductively isolated spawning components form and persist over time. Increased knowledge of cod spawning dynamics can also help to evaluate the conservation risks associated with management options and help minimize the probability of fishery-induced alterations of spawning behavior or population structure (Rowe and Hutchings 2003).

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