The application of small scale fishery closures to protect Atlantic cod spawning aggregations in the inshore Gulf of Maine

Michael P. Armstrong a,*, Michal J. Dean a, William S. Hoffman a, Douglas R. Zemeckis b, Thomas A. Nies c, David E. Pierce d, Paul J. Diodati d, Daniel J. McKiernan d

a Massachusetts Division of Marine Fisheries, Annisquam River Marine Fisheries Station, 30 Emerson Avenue, Gloucester, MA 01930, USA
b University of Massachusetts-Dartmouth, School of Marine Science and Technology, 706 South Rodney French Boulevard, New Bedford, MA 02744, USA
c New England Fisheries Management Council, 50 Water Street, Mill 2, Newburyport, MA 01950, USA
d Massachusetts Division of Marine Fisheries, 251 Causeway Street, Suite 400, Boston, MA 02114, USA

ARTICLE INFO

Article history:
Received 19 October 2011
Received in revised form 21 September 2012
Accepted 24 September 2012

Keywords:
Atlantic cod
Gadus morhua
Spawning closure
Gulf of Maine
Fine-scale management
Population structure

ABSTRACT

Atlantic cod (Gadus morhua) spawning aggregations in locations and seasons that are persistent from year to year and individual fish have been shown to exhibit spawning site fidelity and home to specific spawning grounds each season. In the Gulf of Maine, cod are known to have historically occupied a mosaic of spawning grounds but many of these spawning components have been extirpated, primarily through overfishing, with a near complete loss of spawning along mid-coast and eastern Maine. The remaining spawning aggregations in the western Gulf of Maine are particularly vulnerable to over-exploitation owing to their proximity to shore, the predictability of their timing, the fine-scales upon which they operate, and the high density of fish within each aggregation. Broad scale management actions that are currently being discussed may allow an increased harvest from these spawning aggregations. In this paper we describe the creation of three small-scale area closures that serve to eliminate the exploitation and disturbance of discrete spawning aggregations of Atlantic cod and prevent the potential extirpation of these spawning components. Each closure was unique in the circumstances that surrounded their creation, including differences in the amount of prior protection from commercial and recreational exploitation, the timing and duration of the closure, the size of the closure area, the management body that had authority to enact the closure, the amount of monitoring that has occurred, and the amount of spatial or temporal modifications that have occurred since enactment. We believe the case for spawning closures for Atlantic cod has already been made by several authors and the purpose of this paper is not to present new science, but rather to show the path that was followed to create these spawning closures within the complicated array of fisheries management.

Published by Elsevier B.V.

1. Introduction

Recent efforts to manage and rebuild the Gulf of Maine (GOM) stock of Atlantic cod (Gadus morhua) have been based on reducing and controlling the fishing mortality rate (F) across the range of the stock (NEFMC, 1985). The assumption has been that a reduced F would result in growth of the stock to the target biomass, SSBm(t) (the spawning stock biomass that produces maximum sustainable yield). This classical approach of simply controlling the fishing mortality rate to rebuild the stock has resulted in limited success. Despite reductions in landings and fishing effort, the most recent stock assessment for the GOM cod stock indicates that spawning stock biomass (SSB) has increased only slightly over the last fifteen years, and the stock remains in an overfished state (<1/2 SSBm(t)) and overfishing continues to occur (F= 1.48) (Northeast Fisheries Science Centre, 2012).

GOM cod is one of twenty demersal stocks regulated by the Northeast Multispecies Fishery Management Plan (FMP). From 1994 to 2009, the FMP relied on a complicated system of fishing effort controls. These included a series of large seasonal closed areas (henceforth referred to as “Rolling Closures”) in the inshore GOM (Fig. 1) that were added in 1998 and 1999 in response to the ineffectiveness of more direct controls such as trip limits, minimum sizes, and days at sea limits (Murawski et al., 2000). While these closures were originally designed to reduce fishing mortality on seasonal aggregations of cod, over time the closures were modified to reduce fishing effort on a wide range of stocks. The closures targeted areas of high catch rates but were not explicitly intended to protect spawning aggregations. These closures only applied to commercial fishing vessels and did not constrain recreational activity, which included for-hire vessels. Beginning in 2010, management of the commercial fishery underwent a dramatic change, shifting
from primarily effort controls to a catch-share system that relies on quotas to control fishing mortality (NOAA, 2010). As a consequence, many commercial vessels in the catch-share system were given access to some of the Rolling Closures in nearshore areas.

Currently, managers are considering lifting additional Rolling Closures under the assumption that they are no longer necessary given that harvest is now controlled by hard quotas, as administered through catch shares. However, recent advances in the understanding of Atlantic cod population structure in the region (Wirgin et al., 2007; Ames, 2004; Kovach et al., 2010) have indicated that explicit protection of spawning aggregations needs to be considered and the protection afforded by Rolling Closures should be maintained perhaps on a smaller scale than previous closures.

Throughout their range, Atlantic cod form spawning aggregations in locations and seasons that are persistent from year to year (Robichaud and Rose, 2001; Wright et al., 2006; Vitale et al., 2008; Meager et al., 2010; Skjæraasen et al., 2011). Additionally, individual fish have been shown to exhibit spawning site fidelity and home to specific spawning grounds each season (Robichaud and Rose, 2001; Howell et al., 2008; Skjæraasen et al., 2011). In the GOM, cod are known to have historically occupied a mosaic of spawning grounds (Bigelow and Schroeder, 1953; Ames, 2004; O’Brien et al., 2005), and the stock has been described as a metapopulation, where individual spawning components function as subpopulations (Wright et al., 2006). However, many of the historic spawning components have been extirpated, primarily through overfishing, including nearly half of all spawning components in the GOM and a near complete loss of spawning along mid-coast and eastern Maine (Ames, 2004). Those spawning components that remain active are concentrated in the southern GOM and appear to occur on much smaller spatial scales than those described in historic documents (Bigelow and Schroeder, 1953). These well-defined spawning aggregations are particularly vulnerable to over-exploitation owing to their proximity to shore, the predictability of their timing, the fine-scales upon which they operate, and the high density of fish within each aggregation (Bigelow and Schroeder, 1953).

Although Atlantic cod in the GOM have been treated as a single stock for assessment and management purposes, recent genetic studies identify significant intra-specific diversity in US waters (Wirgin et al., 2007; Kovach et al., 2010). Much of this diversity is believed to be a result of the temporal and spatial variability in spawning (Howell et al., 2008; Kovach et al., 2010), spawning site fidelity (Perkins et al., 1997; Howell et al., 2008), and larval dispersal dynamics (Huret et al., 2007; Churchill et al., 2011). Therefore, the remaining spawning components demand robust protection from over-exploitation in order to maintain this diversity and prevent further collapse of population structure.

In recent years, additional protection has been applied to these aggregations by management agencies. Here we present three case studies where small scale spawning closures have been implemented, with each case varying in the circumstances surrounding their enactment. We describe the processes by which the areas were identified, how the closure boundaries were initially delineated and then spatially and temporally refined, the monitoring that has been conducted, and the benefits that we believe have been accrued as a result of these actions. We believe the case for spawning closures for Atlantic cod has already been made by several authors and the purpose of this paper is not to present new
science, but rather to show the path that was followed to create these spawning closures within the complicated array of fisheries management.

2. Case studies

2.1. Case study 1: the Massachusetts Bay Winter Cod Conservation Zone (WCCZ)

In this case study, an area was initially closed simply to reduce gear conflicts and trip limit overages, but morphed into a spawning area closure when it became apparent that the fishery was exploiting a cod spawning aggregation. The closure affected both the recreational and commercial fisheries.

In late fall of 2002 and 2003, staff from the Massachusetts Division of Marine Fisheries (MADMF) observed a dramatic increase in recreational and commercial fishing effort in an area located about 15 km northeast of Boston, Massachusetts in western Massachusetts Bay. During November of those years, the recreational fishing fleet was observed concentrated on dense aggregations of Atlantic cod (Fig. 2). In December, the Rolling Closures lifted and the area became open to the commercial fishing fleet which targeted the same aggregations using sink gillnets, longlines, and rod and reel. At sea observations indicated large amounts (100’s to 1000’s kg) of dead discard of cod from the gillnet fleet owing to low trip limits, and conflicts arose between the recreational and commercial fleets and among the commercial gear types.

In the fall of 2003, an Industry-Based Survey (IBS) for Atlantic cod in the GOM was initiated to better characterize the spatial and temporal distribution of this stock, including the identification of potential locations of spawning activity. The survey confirmed an abundance of pre-spawning cod in Massachusetts state waters in northern Massachusetts Bay during November of 2003 (Hoffman et al., 2012). Based on this information and on observations of the commercial and recreational fleets, the Massachusetts Division of Marine Fisheries enacted an emergency closure of a small area (Fig. 3) from December 16, 2003 to March 31, 2004. The closure prohibited the use of gears that could catch cod and encompassed an area of about 140 km², extending from the shore to about 10 km out to sea.

In the following December (2004), the commercial and recreational fleets began fishing on another spawning aggregation, located adjacent to the area that was closed the prior winter, between the eastern boundary of that closure and the state waters line. At the end of December, the MADMF again moved to enact an emergency closure, expanding the boundary to the east to
encompass the additional cod aggregation. However, before this rule was enacted, information from at sea observers and enforcement officers indicated that the fleet had dispersed in response to reduced catch rates, a likely indication that much of the spawning aggregation had been caught or dispersed, so in the end, no rule was finalized.

In the fall of 2005, the MADMF promulgated rules to create the permanent Winter Cod Conservation Zone (WCCZ) (Fig. 3), with the final boundaries delineated based on prior years’ observations on the location of the fishery by staff of the MADMF, federal sea sampling, and environmental police officers. This information was supplemented with data from the IBS and the MADMF inshore trawl survey. The northern and southern boundaries provided an approximate 3 km buffer around all observed aggregations and were coincident with major lines of latitude for ease of compliance and enforcement. The closure was bounded to the west by the shoreline and to the east by the Massachusetts state waters line (Fig. 3). The WCCZ closure dates were set as November 15–January 31, two months shorter than the time period in the previous emergency closure (November 15–March 31). This reduction of the closure period was based on observations of the prior monitoring programs, which indicated that all spawning activity in this area was over by the beginning of February.

The MADMF has conducted bioacoustic surveys during December of most years since 2005 to verify the continued presence of spawning aggregations within the boundaries of the WCCZ and to pinpoint their positions (Fig. 4 is an example echogram obtained during a survey showing a cod concentration about 8 m in height). The Massachusetts Environmental Police monitors the area each year during the closure period (November 15–January 31) through routine boat patrols to prevent illegal fishing. The MADMF monitors sea sampling reports from fishing activities outside the WCCZ to identify any additional spawning aggregations beyond the boundaries of the closure that would necessitate a restructuring of the borders. In 2011, the size of the WCCZ was reduced slightly by moving the southern boundary about 2 km to the north and eliminating the northeast corner of the closure area (Fig. 3). These refinements were based on observations from fishermen, fisheries observers, and the IBS trawl survey data, which all indicated that these areas contained few spawning cod. These small changes were intended to provide fishermen with increased opportunity to catch other species while still maintaining protection for spawning aggregations of cod.

2.2. Case study 2: the Massachusetts Bay Spring Cod Conservation Zone (SCCZ)

In this case study, the spawning aggregation was identified through acoustic surveys prior to the intensification of recreational fishing effort over several years. The closure was in direct response to this large increase in recreational fishing effort directed on the spawning aggregation.

Through bioacoustic surveys of potential nearshore cod habitat during 2004–2005, the MADMF staff identified a spring aggregation of spawning fish that was concentrated in a small area about 0.15 km² in size situated 5 km from shore. The MADMF closely monitored the fishing activity in the area from 2006 to 2008. During that period, recreational activity increased considerably, attributable to increased knowledge of the aggregation through word of mouth and on the water observations of fishing activity. This area is in the Rolling Closures and so it has been closed to commercial activity during May and June. Nonetheless, the MADMF staff repeatedly observed commercial fishermen harvesting cod from the aggregation under the guise of recreational angling. At the time, the recreational bag limit was 10 fish per person per day. A small commercial vessel fishing with multiple persons on-board could retain commercial quantities of cod. For example, a boat with 4 persons on-board could legally harvest 40 large cod (equal to about 375–550 kg round weight) by rod and reel and then sell them illegally when they reached port by simply declaring that they were caught from a different area. Because of the difficulty in distinguishing recreational from commercial fishing activity, on the water enforcement was ineffective. In 2009, the MADMF, based on concerns of over-exploitation of this aggregation resulting from this concentrated recreational and illegal commercial harvest, created the permanent Spring Cod Conservation Zone (SCCZ) (Fig. 5).

The SCCZ was centered where dense aggregations of cod in spawning condition had gathered over the previous three years. The closure was constructed as a box that coincided with lines of latitude/longitude for ease of compliance by the recreational fleet. Also, the closure was sized to allow a minimum buffer of at least 2 km in all directions around the aggregation (Fig. 5) and the initial closure dates were May 1–June 30.

A research program was initiated by the MADMF to monitor and to better characterize the spawning aggregation. Bioacoustic surveys were conducted each year during April through July to verify the continued presence of spawning aggregations within
the boundaries of the closure and to localize their positions. Additionally, a drop camera was used to record video images of the aggregation to confirm species identity (Fig. 6). These surveys indicated that cod aggregations were present before and after the initial closures dates (May 1–June 30) so, in 2011, the closure dates were expanded to April 15–July 21.

From 2009 to 2012, spawning cod were tagged using conventional t-bar tags, data storage tags (DST’s), and acoustic transmitter tags. The acoustic transmitter tags were used to examine movements on the spawning grounds and are being used to investigate spawning site fidelity and spawning behavior, whereas, the t-bar tags and DST’s are being be used to investigate movements off the spawning grounds. Several papers are in preparation presenting the results of these studies.

The movement of cod on the spawning grounds was determined using a vemco positioning system (VPS). This system used a 28-receiver array, which was set in a 2 km square surrounding the central location of the spawning aggregation, to triangulate the location of acoustic tag signals. These data indicated that part of the spawning aggregation left the main group each evening and moved out of the closure area to the east and west (Dean et al., in preparation). In response to this information, in 2011, the boundaries of the closure were moved 1 km to the east and west.

The ability to track the movements of cod on the spawning grounds using acoustic telemetry allowed us to observe the reaction of individuals in the aggregation to the opening of a concentrated sink gillnet fishery on July 1, 2009. Individuals showed an immediate increase in movements when the gillnets were set and within eighteen hours of the fishery opening, all tagged fish on the spawning ground were either caught in a gillnet or had permanently left the area, indicating total disruption of the spawning aggregation (Dean et al., 2012). Similarly, fishing activity with trawl gear has also been documented to disrupt cod spawning aggregations (Morgan et al., 1997). Therefore empirical evidence suggests that over-harvest is not the only concern with respect to cod spawning aggregations, but negative effects from fishing activity can also alter the spawning behavior of cod and reduce their reproductive success.

At the time of this writing, the MADMF is contemplating a significant increase in the size of the SCCZ in response to the results of at-sea sampling aboard commercial vessels during May–June, 2011, where the presence of another spawning aggregation was identified in an area a few km south of the SCCZ that was recently opened under a state waters experimental fishery.

2.3. Case study 3: the Gulf of Maine Cod Spawning Protection Area (CSPA)

Similar to case study 2, this closure was initiated primarily in response to significantly increasing recreational fishing pressure on a cod spawning aggregation. Whereas the WCCZ and SCCZ were implemented in state waters through the authority of the Massachusetts Division of Marine Fisheries, the Gulf of Maine Cod Spawning Protection Area (CSPA) was located in federal waters and was implemented by a collaborative effort among the states through the New England Fisheries Management Council (NEFMC) and the National Marine Fisheries Service (NMFS).

In June of 2010, the MADMF alerted the NEFMC to increased recreational fishing activity (Fig. 7) in an area of Ipswich Bay known as Whaleback, located about 12 km from shore. Concerns regarding the vulnerability of the spawning aggregations in this region to extirpation were heightened by the realization that with the newly implemented commercial catch-share system there would be the
potential for intense commercial fishing pressure in this area. As a result, the NEFMC agreed to develop a closure to protect these spawning aggregations. In a significant change from past federal practices in the GOM, the closure was planned to apply to both commercial and recreational vessels. Based upon results from recent research (Howell et al., 2008; Howell, 2009), the technical staff of the NEFMC began to work with interested individuals from the commercial and recreational sectors to design an appropriate closure area. Several alternatives were developed over the course of the summer. The alternatives tried to balance the research results, ease of enforcement, and need for continued access to other species.

By the fall of 2010, the NEFMC had developed a preferred alternative (Fig. 8). The area was designed to provide protection to spawning cod by limiting fishing in an area during which times the catch rates were high, by eliminating the targeting of large repeat spawners and preventing fishing from interfering with spawning activity. In addition, the closure was designed to be large enough (both in time and area) to allow cod some opportunity to disperse before being subjected to fishing pressure. Since this was the first time the NEFMC was proposing a closure for recreational vessels fishing in federal waters in the GOM, there were concerns that recreational interests were not aware of the ongoing deliberations.

Working with the States of New Hampshire and Massachusetts, the staff of the NEFMC held a series of informal meetings to brief the recreational sector on the proposed closure and reached out to the industry through on-line discussion groups before their final decision was reached. The proposal was met with little opposition and in November 2010 the measure was adopted by the NEFMC and submitted to the National Marine Fisheries Service (NMFS) for approval and implementation. The regulations were in place by the start of the fishing year on May 1, 2011. Researchers from the University of New Hampshire initiated efforts in 2011 to estimate standing biomass based on bioacoustic surveys (W. H. Howell, University of New Hampshire, personal communication). Additionally, in May of 2012 researchers from the MADMF and the University of Massachusetts – Dartmouth began conducting bioacoustic surveys to locate and estimate relative abundance of cod aggregations in the CSPA as part of a study to document movements and spawning behaviors.

Anecdotally, we have been informed by some recreational fishermen that the boundaries are hard to locate on the water because they are based on loran lines rather than latitude and longitude. There have also been suggestions from industry members that the area needs to be expanded in order to provide broader protection of the aggregation. However, because the closure is so recent, no discussions have been held regarding refinements that could be done on the boundaries.

3. Discussion

Here we describe the creation of three small-scale area closures that serve to eliminate the exploitation and disturbance of discrete spawning aggregations of Atlantic cod. Each closure was unique in the circumstances that surrounded their creation, including differences in the amount of prior protection from commercial and recreational exploitation, the timing and duration of the closure, the size of the closure area, the management body that had authority to enact the closure, the amount of monitoring that has occurred, and the amount of spatial or temporal modifications that have occurred since enactment (Table 1). The spawning aggregation in the WCCZ occurs in December–January and was not previously protected by seasonal area closures. Prior to implementation of the WCCZ, the aggregation was heavily exploited by both the commercial and recreational fleets. The spawning aggregation in the SCCZ occurs in mid-April to mid–July and was previously protected from commercial fishing by Rolling Closures during May and June but was vulnerable in April and July. The area was open to recreational fishing and also exploited by illegal commercial fishing masked as recreational activity. Both the WCCZ and SCCZ areas are located in the state waters portion of Massachusetts Bay and so the closures were enacted through rule making by the MADMF only. The spawning aggregation in the CSPA also occurs in mid–April to Mid-July and so was afforded partial protection from commercial exploitation by seasonal area closures but was heavily exploited by the recreational fleet through both private and for-hire vessels. Because the location of the spawning aggregation was in federal waters, the process to enact an area closure needed to go through the NEFMC and the NMFS. Although the state (MADMF) and federal (NEFMC/NMFS) processes for establishing rules were quite different, the actual reasons and rationale for establishing the closures were the same: to protect spawning aggregations of Atlantic cod that were being exploited in an unsustainable manner by both the recreational and commercial fleets. In all instances, the locations of the spawning aggregations, as well as the closure boundaries and timing, were established through sound science with additional input and cooperation from commercial and recreational fishermen.

Monitoring of the spawning aggregations and the fishing fleets has been important since the closures were created and we regard pre- and post action monitoring as a necessary component of any plan to create area spawning closures. The monitoring served to ensure that the boundaries of the closure were properly located. In the case of the SCCZ, the area was enlarged and the closure dates expanded in response to the results of monitoring, while the WCCZ was decreased in size two years after the initial closure. These changes in the closure parameters were readily accepted by fishermen, because they were based on strong empirical evidence supplied through monitoring. Monitoring efforts also identified the negative effects of the opening of a gillnet fishery on a cod spawning aggregation (Dean et al., 2012).

Sadovy and Domeier (2005) discussed the risks of overexploitation and loss of genetic diversity by fishing on spawning aggregations of reef fishes, and we believe that the same risks exist for temperate fishes such as Atlantic cod. It has been noted that the benefits of small closures to protect spawning aggregations are
negated if the fish are simply caught elsewhere after leaving the spawning aggregation (West et al., 2009). However, for fish such as Atlantic cod, which spawn in dense, predictable aggregations (Rose, 1993), and exhibit complex spawning behavior (Brawn, 1961) that can be interrupted by fishing activity (Morgan et al., 1997; Dean et al., 2012), small-scale spawning closures offer significant protection of spawning aggregations and are effective management strategies to prevent over-exploitation.

For fisheries managed by quotas, a displacement of the fleet from one locality to another, where the same population is fished, will generally have little effect on F if the same quota is taken (Hawood et al., 1998). However, in the case of Atlantic cod, spawning closures force the fishery to occur when cod move away from the spawning site (Perkins et al., 1997; Howell et al., 2008) and mix with cod from different spawning components on offshore spawning grounds (Hunt et al., 1999; Tallack et al., 2008). Therefore, the fishing mortality is presumably distributed across many subpopulations of cod, reducing the likelihood of extirpating any individual spawning component which would result in further collapse of population structure and a reduction in reproductive capacity (Rose et al., 2008). The net result of a reduced F and the protection of cod spawning aggregations is the preservation and restoration of genetic diversity and population structure, as well as a more robust age structure with increased spawning diversity resulting in greater overall stability of the GOM stock of Atlantic cod (Kerr et al., 2010).

Depletion of the historic spawning components may be the result of managing the GOM stock of Atlantic cod as a single stock with no consideration of the complex stock structure (Reich and DeAlteris, 2009) and a failure to acknowledge biologically meaningful populations (Kovach et al., 2010). In fact, managing the stock as if it were one large stock likely overestimates the potential for growth and harvest (Sterner, 2007) and compromises future fishery yields. Under this system, the identification and protection of individual spawning aggregations is critical.

While we have successfully instituted protection for three active nearshore spawning aggregations, there are no doubt additional aggregations in the GOM that require similar protection. These aggregations need to be identified as fishing effort may be refocused upon these due to the current spawning area closures. These aggregations may be more difficult to identify as at least some of them are likely further from shore, on offshore banks. Efforts to identify these areas need to utilize a variety of data sources including trawl surveys, sea sampling, vessel trip reports from commercial and recreational for-hire boats, the cod IBS (Hoffman et al., 2012), and anecdotal reports from fishermen. This should be followed by biological sampling in areas of high cod concentration to identify the reproductive status of cod in those areas. Areas demonstrated to contain high concentrations of cod in spawning condition should be considered for inclusion in future closures.

Small area closures for the explicit purpose of protecting Atlantic cod spawning aggregations in the GOM is an important new tool in the toolbox of fisheries managers as they strive to achieve a stable, robust stock. Ironically, spawning closures were considered an important management tool for groundfish in the GOM long before the advent of modern fisheries science and management. In 1668 the Massachusetts legislature, in recognition of the importance of the nearshore winter spawning aggregations, issued the following law: “...that no man shall henceforth kill any codfish, hake, haddock, or pollack to dry for sale in the month of December or January because of their spawning tyme. . .” (see Claesson et al., 2010). While this colonial law was lost as Massachustts transitioned from a colony to a state in the late 1700’s, by instituting the spawning closures outlined in this paper, we have mirrored the actions of our forefathers. Management of Atlantic cod at a large scale has failed to prevent the loss of spawning components (Smedbol and Stephenson, 2001). While the realities of fisheries
management mean that it is unlikely that Atlantic cod can ever be managed at a scale appropriate to their population complexity in the GOM, careful monitoring, preservation, and restoration of spawning aggregations should be a priority of the management bodies and it is believed to be critical to the restoration of historic stock structure and biomass.

Acknowledgements

This is Massachusetts Division of Marine Fisheries Contribution No. 37. We thank Brad Schondelmeier, Brant McAfee, Gary Nelson, Brian Castonguay, Matt Ayer and many other MADMF employees who assisted in monitoring efforts. We thank Melanie Griffin and Jared Silva for their help in implementing the closure regulations. Jeanne Shaw provided helpful editorial comments on the manuscript. We thank Steve Cadrin and Dave Martins for their input and support of research concerning spawning closures and cod aggregations. The editors (Rachel Feeney and Ken LaValley) and two anonymous reviewers provided comments that significantly improved the manuscript. This project was partially funded by the U.S. Fish and Wildlife Service through the Sportfish Restoration Act, grant F57R, provided to the Massachusetts Division of Marine Fisheries.

References