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Exploring Fine-scale Ecology for Groundfish In the Gulf of Maine and Georges Bank

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Workshop Summary

The Gulf of Maine ecosystem is among the most complex and well-studied bioregions in the world. However, the groundfish fishery that was once the mainstay of many coastal communities remains vastly diminished. In response, some have called for a re-evaluation of the scale at which we manage fisheries. Over the last decade considerable research has accumulated on the groundfish species within the Gulf of Maine region migration, abundance, and habitats have all been explored. When considered in the context of the broader system, this work may provide new insights on ecologically appropriate scales for management.

The Gulf of Maine Research Institute, Penobscot East Resource Center, the Maine Department of Marine Resources, Maine Sea Grant, and the University of Maine convened a workshop entitled "Exploring Fine Scale Ecology for Groundfish in the Gulf of Maine and Georges Bank" on April 2-3, 2009 in York, Maine. The workshop brought together fishermen, oceanographers, biologists, social scientists and managers for a rich discussion on what is known and what questions remain to be addressed to manage groundfish within the Gulf of Maine at multiple scales.

Keynote: Current Assessment Structure

Steve Murawski
Director of Scientific Programs and Chief Science Advisor
NOAA Fisheries

Dr. Murawski outlined his talk, which would cover where we have been in terms of spatial scale, where we are now, and where we might head in the future. He noted that science can occasionally get ahead of management, and when developing a new management system, it is important not to overrun the ability to monitor. Yet, things are very dynamic right now and there is a lot going on in spatially explicit management, so this workshop is very timely.

Murawski began by covering definitions of biodiversity and managing to scale by using examples outside of groundfish. These concepts are often mixed up and we've not been able to identify sub-population or stock definitions. Population is a definition of a reproductively isolated segment of the species. In New England, we do stock management. For a variety of reasons, we choose not to sort them out into distinct populations for management purposes. What is this workshop seeking? Are we trying to look at finer scale management units or sub-stock units? If we want to make biology and management float together, ideally you would get a management unit that is parallel to biological characteristics. However, we do not have to limit ourselves to talking about biology just because we want to talk about finer-scale management.

He then turned to the historical basis for management unit definition for New England Groundfish. You'll see a trend in haddock, looking at the "crash" in 1929. This set off modern fishery biology in (New England?). The first time we saw a map of the statistical reporting areas was in the 1930's when Harrington started to work on haddock. These were first statistical areas were designated by the North American Council on Fishery Investigations (NACFI). Early Canadian landings data was only delineated by inshore/offshore, which was not even recorded in miles. Trawling was not allowed until the 1950's, so this was a fixed gear fishery both inshore and offshore. The ICNAF reporting scheme was the guidepost from the early 1950's to present. We based reporting areas on those stock boundaries, but the science was evolving and very little was known about stock structure dynamics when this was developed. There's been a lot of work looking at these boundaries in more detail, but early data gave us one perspective. While we all share concerns about shifting baselines, the fact is that the data then was not what it is now and we have to deal with that reality.

The stock units used in the northeast multi-species complex are well demonstrated by a few examples. One of the confounding stock groups is yellowtail flounder, which include Cape Cod/Gulf of Maine, Georges Bank and Southern New England/Massachusetts. These stocks are interesting because they converge on one spot in the ocean and of course fish don't know where the boundaries are. We know from tagging efforts that the stock allocation information is not precise, but does it all come out in the wash? That is unlikely, of course, because of differential abundance – the rates and magnitude may be different. This represents a nuance of trying to tease out more information from statistical areas. Genetic work here does not allow enough precision, unlike the west coast, where there's sufficient differentiation and we're close to having near real-time methodology, even though it's very expensive. We must ask ourselves if that cost is worth the knowledge it imparts, or is it good enough to look at it the way we do here in New England? The more precision we need, the more it will cost. The more sub-stocks we want to sort out, the more detailed tools we will need to identify them.

Turning to cod, we have the Georges Bank and Gulf of Maine stocks. There are other cod groups as well. If you look at early life history—distribution of eggs and larvae—there is lots of opportunity for mixing because eggs and larvae are in water column for a long time, particularly on Georges Bank where there's a circular current pattern. Looking at haddock -- and to some extent, cod -- it's the settling out process where you start to get differences. They are not reproductively isolated. The current basis for stock groups is based on tagging studies done in early years (Schroeder, NACFI), which indicated areas of retention but a lot of straying back and forth, and parasite infestation research, spawning time data, and growth rate analyses. Cod is a much larger metapopulation in the West Atlantic, including about 12 stocks. As people started to tag animals in Newfoundland and elsewhere, we have seen straying throughout this area. If you have 12 stocks, how much synchrony is there between them? If they were truly distinct, you wouldn't see much. If you look at landings history over 100 years, things move along at a stable level and then there is a big trace form the distant water fleets, some recovery, and then they all go down at the same time. Yet in the landings data, there is a fair amount of synchrony, so they seem to be reacting to a lot of the same stimuli. They are not populations that are completely isolated. We also see high correlations in survivorship of juveniles of haddock.

If you're going to manage to sub-stocks, you also need to look at the drivers. It is important not to move to finer scale management without referencing what is going on in adjacent things as well. It is critical to take advantage of what's going on in the larger scale system in order to manage at a finer scale.

Redfish provides a cautionary tail in terms of population dynamics. The industry started off in Gloucester, catching redfish close to home. Landings went up quickly, but we saw a serial depletion effect because redfish are schooling fish and easy to catch. There was identity to individual sand banks or features, but when landings declined they fishery moved further and further east. We do not know what the sub-stock structure was, though we have started to see a dramatic recovery, almost to BMSY. It gives us a chance to go back and look at those banks and schools to see if we can reconstruct sub-stock structure that was invoked as the decline occurred. Perhaps we do not have the diversity now that we had then, and perhaps we fished out those pockets, leaving us with more homogenous stocks. Redfish never made it to total collapse so it may be a better example than cod to look at recovered sub-stocks, but we won't know.

New England has the most complex system of spatial management Murawski has seen, given the seasonal and rotating closures. It is very confusing, and we're obviously trying to accomplish a suite of objectives for 19 different stocks. If we look more generically at the United States, 67% of the EEZ (about half on the west coast area) is closed to trawling for various reasons. There are many good examples of the impacts of spatially explicit management on maintenance and recovery of stocks. Sedentary species have been interesting examples of spatial management. Spatial management has been a successful regime for scallops, as closed areas validated natural mortality rates and growth rates.

What about other species? If you look at a plot of trawling effort around closures in New England, you see interesting movements. VMS data can be married with observer coverage in order to sort out catch rates relative to closed areas. This shows animals may be setting up sub-population structures relative to the closed areas. Haddock is clearly a species where there's availability to have spatial substructure but that's not the case for all groundfish species. Some catch rates actually go up the further you get from the closed areas. If we want to use spatial management, it needs to be for species that are halfway down the sedentary spectrum, like haddock and yellowtail. Cod move around much more, and they aren't spending a lot of residence time in closed areas. Some species are attracted to closed areas and others are repelled. Because of the haddock effect, it's more effective to fish close to the closed area lines. Cod, pollock and hake will be repelled. We have looked at residence time calculations using acoustic tags and with more information our understanding continues to grow, but we need to recognize that closed areas are not necessarily going to be gardens of diversity. In order to do spatially explicit management, these effects are important to understand and examine. Trawl survey data shows not only what is outside the closed areas, but also what is inside, giving two windows for understanding this data. Fishermen's catch rate data is more precise because there were more tows. It is based on the amount of information that we get such richness from the conclusions. Closed areas effectively just switch effort back and forth, so you have to question the net conservation value of these closures. These closures may concentrate things like yellowtail, and the fishermen see that.

The US/CA resource sharing agreement for (cod, haddock, and yellowtail flounder) says we will partition the area for purposes of partitioning landings data, though we recognize that we have to manage other parts of the puzzle on the western side. In any kind of sharing agreement, you can't exceed the biological reference points. If we want to partition into smaller areas, we need to consider the impact on the overall region, because you don't want to overfish areas in pieces. If we partition into smaller areas or amounts, we need to be sure we can put the populations back together without overfishing them.

Turning to Pacific groundfish, rockfish larvae disperse widely even though stocks are relatively sedentary. A group of fishers in Half Moon Bay want to form a sector to address their concerns about preserving access to the fishery before it is taken by other fishers further away. They're trying to get a community allocation. Appropriateness of spatial data on the west coast is related to the thin coastline. If you start with observer data, you can overlay it on statistical areas and look at start and end of each tow. High-resolution habitat maps show habitat under each tow. Pacific coast managers want to move trawling off the hard rocky bottom onto more appropriate habitat. In earlier years, there was lots of trawling through rocky bottom, but data availability has allowed industry to avoid those hard bottom nursery areas. This helps to achieve conservation objectives over and above stock conservation efforts. Depth strata also show amounts of area closed by depth.

In the current state of science for stock definition and spatial management, Murawski believes we are going to see increased discussion about managing space in addition to managing fish. If we're going to preserve fishing opportunities, we're going to have to come to the table with information on a spatial level. Looking to the future, more precise fishery dependent data is now feasible. How can we build bridges to historical data when the information was not that precise so that we can make use of it? Newer information is better and more precise, but Murawski does not find it revolutionary -- recent tagging studies give roughly similar results to historical studies. Do we have technology to be more precise at a low cost? Not right now. So is it worth it here, as it is worth it when you're fishing endangered species on the west coast? How can we define sectors and management units to allow biological diversity to be maintained while supporting local communities? Murawski challenged the group assembled to address these trigger questions over the course of the workshop.

Q: *As we move perhaps toward fine scale management, how to managers determine what kind of management is required to make decisions?*

A: Obviously there are some precision tradeoffs and from a scientific perspective we want as much information as possible. What should we prioritize? We're dealing with a fishery dependent data system in transition. Historical data is very consistent, but not precise. Now we have the tools and technology to get very precise data, and it is worth getting good data – the fishery has very high value potential.

Q: *Some of the questions you posed are going to require leaps of faith from management. For example, closing mid-water trawling in groundfish closed areas. Will we wait for the science?*

A: You raise an important point. In crude terms, all of what we are doing is experimental management. We often don't understand the ways different species and stocks will benefit. The next generation of closed areas will be more targeted and more precise. We are doing adaptive management and learn these lessons.

Q: *More spatial science is expensive, but I think we may be collecting more spatial information than we're using. There are costs to getting it, but also costs to not considering it.*

A: Surveys weren't designed for looking at spatial patterns, but rather for long time monitoring. One thing we can do with observer data is actually show movement patterns that you interpolate from seasonal surveys. We have moved from taking a snapshot picture to understanding real-time dynamics. The challenge is to have dynamic models.

Q: *You discussed the potential effect of closed areas on sedentary species selecting for sedentary lifestyles. What if we can show that closed areas are selecting for those species? Do we then close areas for more migratory species?*

A: We have not been selective about how we deal with closed areas—we just keep layering them on. So what do we do about migrating species? We could look at terrestrial management and create migratory corridors (though fish don't know where those corridors are), and it's not quite like they are following a highway. If you leave parts of the path open, it will attract fishing effort. Overall, we need to be more careful about layering on more closures and figure out what the low hanging fruit is with closed areas—it's a very allocative tool and pushes people to larger boats able to move with closures.

Q: *I am interested in the synchrony data. I have gone over Rothschild's conclusions, which are similar, and my concern was that he was looking at large management units. If you have demographic structure at a finer scale but you homogenize the larger areas, what impact does the fact that they are nested have? Do you start to homogenize the finer structure, or local stocks?*

A: What does synchrony tell us? Probably that there is a climatic signal. There was a big signal from distant water fleets, but there are certainly asynchronous signals and asynchronous behaviors as you get to more local populations. But can you manage to it, and regulate it? You are then talking about tracking in real time. Which is not to say that you can't do it, and your point is a good one. That data is from the stock assessment, and so if you want to track at a finer scale, you might have to go to landings data. The time series won't be as long.

Q: *In your opinion, what are the two highest priority research questions this region should be focusing on?*

A: We need to figure out ways to incorporate much more precise fishery dependent data.

Panel: Tagging and Stock Structure Studies

Don Clark, Department of Fisheries and Oceans, Canada

Dr. Clark began by talking about relevant scale. Looking at overall work on cod populations, there is evidence of some discrete areas, and while the population is not entirely homogenous, it is not distinct either. The work Dr. Clark has done is mostly in the Bay of Fundy and Scotian Shelf area. There is a lot of movement from the Scotian Shelf across to Georges Bank. Fish there were different enough to be identified by size and even condition (they are fatter on the Scotian Shelf) within the same year class. We have tagged cod collaboratively within the region since 2001, mostly with commercial fishermen, fairly broadly in order to see what kind of resolution we would get from the results. Tagging resumed again in 2003 through participation in the Northeast Regional Cod Tagging Program; this time tags were deployed during trips on DFO research vessels only. These more recent tagging efforts attempted to resolve the different components seen in 4x by focusing on the Digby Neck/Bay of Fundy area.

Clark's general results showed that cod released east of Browns Bank were returned primarily from eastern 4x. Tags from Browns Bank come from pretty much everywhere, so tagging between areas, fish seem to go both ways. Looking at this data, Clark found different patterns in returns even from fish tagged in the same areas within a week of each other, reflecting finer scale differences in movement patterns. In the Bay of Fundy, we're seeing very little mixing. In the summer, most fish were tagged and recaptured/reported from the same place, though movement in the winter showed greater dispersal. Returns from the south shore of Nova Scotia showed limited movement, with almost all returns coming from within 20 miles of the coast. So while some areas show very migratory fish, other areas show less movement. In conclusion, the Bay of undy and Eastern 4x show very little mixing, but cod tagged near boundary are recaptured in both Bay of Fundy/Gulf of Maine and Scotian Shelf.

Do we see the same structure on Georges Bank? [Clark noted that when he speaks of Georges Bank, as a Canadian he is referring to only the eastern end, a much smaller area than many of the workshop attendees would be thinking of.] Fish released on the northern end of the bank in the winter were recovered everywhere. Fish released on the eastern portion of the Bank winter were largely recaptured on the Bank, as were cod tagged on the northern edge in summer. So there may be some fish that stay there all the time and others that are more migratory, so there may be some scale differential on the bank. How localized are differences in movement patterns? Distribution is not discrete, but fish are not mixing completely. Uneven exploitation can occur, resulting in localized depletion.

Canada has also looked at fine scale management for herring. Spawning grounds seem to be fewer in number. We have an overall Total Allowable Catch (TAC) and quotas for individual spawning grounds, restricting fishing from each bed to avoid exploitation. Tagging data can also be used to calculate exploitation rates. However, there are limitations for the use of tagging data. Standard tags cannot be used on small (i.e. sublegal) fish [since they are less likely to be reported from the fisheries], and we do not get returns from areas where fishing doesn't occur (central/eastern Georges Bank), but that does not mean there are no fish there.

So what scale is relevant? A tremendous amount of information can be gleaned from tagging data, some on a broader scale, some on a smaller scale. You need to decide in advance what scale you are interested in when designing a tagging study.

Q: *There are very few returns on the U.S. side in the northern Gulf of Maine. Does this mean that they are not being returned, or what else might it indicate?*

A: It may indicate differences in reporting rates as well as fish not moving across. Tags had two addresses on them (the 2001 tags were orange and showed DFO/Canadian contact information; tags released in 2003 onwards were largely yellow tags with GMRI/US information), and in some areas where we tagged we received almost no returns from across the line.

Shelly Tallack, Gulf of Maine Research Institute

Dr. Tallack began by acknowledging the range of partners who were involved in both tagging and analysis for the Northeast Regional Cod Tagging Program (NRCTP). She then presented tagging as a spatial tool for improving our understanding of fish population dynamics, which looks at short and long term changes in the size and age composition of populations, the biological and environmental processes influencing those changes, and the effects of reporting and mortality. Tagging becomes most useful for looking at growth, immigration and emigration.

The first figure presented shows the raw mark-recapture data, with start and end locations connected by straight lines. Tallack underscored the insufficiency of using this image without examining other aspects of the data; the interpretation of tagging data is obscured by factors such as timing and distribution of tag releases, fishing activity (governed by both regulatory measures and weather) and the compliance of fishermen to report tags.

Tallack and her colleagues have looked at the data in a variety of ways (filtering by fish size, season and release/recapture location) and have proposed core cod migration "passages" based on these raw data. It appears that in the Gulf of Maine, cod "shuffle" back and forth along the Maine/New Hampshire coastline. Some less frequent movements observed showed cod moving out of the near shore waters into the Gulf of Maine, and in the winter of 2004 particularly, cod from the near shore Cape Cod waters moved into near shore southern areas off

Rhode Island. One of the more interesting findings was that cod from the near shore Cape Cod waters show a divergence with some fish recruiting to Georges Bank while others recruit to Gulf of Maine waters; despite this pattern, Cape Cod fish are managed as part of the Georges Bank (5Z) stock. Overall, movement across management areas is obvious and so attempts have been made to quantify these movements as exchange rates between stock management areas; this exchange between areas represents the emigration and immigration component of modeling fish populations. These NRCTP tagging data were recently used in the 2008 Groundfish Assessment Review Meeting (GARM III) and the Transboundary Resource Assessment Committee (TRAC) workshop (January 2009); the analyses were undertaken through lengthy collaborations between the Gulf of Maine Research Institute (GMRI), the Northeast Fisheries Science Center (NEFSC) and the Canadian Department of Fisheries and Oceans (DFO) in St. Andrews, NB. The tagging data were also used to generate growth curves by management area; in one figure Tallack hypothesized how movement may impact growth over a cod's lifespan. The growth trends for Georges Bank (5Z) and the Gulf of Maine (5Y) are consistent with NOAA findings with Georges Bank fish growing faster, but reaching a smaller maximum size.

Tallack reviewed some of the challenges in tagging information to look at stock structure. Many tags (including both conventional and archival tags) require the fish to be recaptured and reported. Tagging data is therefore going to be highly skewed by where fishing activity is occurring; this effect is seen both spatially and temporally as fishermen respond to management tools such as rolling closures or permanent closures. Conventional tags can also only provide a start and end location, so we do not know where fish go between these points when tagged fish are at large for a long period of time. Tallack showed examples of cod at large for >1000 days but which were recaptured within ~10 nm from there release site; "we do not know if they stayed put or moved off and returned". Acoustic tagging technology offers one way around this since the fish do not need to be recaptured to provide information; however acoustic arrays will only observe a fish's movement if it passes through the array. Tallack proposed that now knowing the primary cod migration routes, we are in a better position to set arrays in areas which will capture cod movements. Another option is pop-off satellite tags which are becoming smaller in design, and though they haven't been used on groundfish much to date, we may be able to use these on larger cod.

So what do tagging studies tell us about how 'fine' fine-scale should be? Certainly there is evidence of changes in movement patterns across life history stages, and these changes are probably associated with changes in habitat and foraging needs. The tagging data confirm that dispersal and migration changes with fish size. With regard to reproduction, spawning behavior appears to be very spatially defined. A study by the University of New Hampshire (UNH) confirmed a fine-scale homing behavior in spawning cod, but we don't know if this is applicable throughout the region, and this study cannot tell us what happens to these fish beyond the spawning period - we do not know how far they traveled once they left the acoustic detection area. We still need more information on natal homing for the Gulf of Maine region before we can fully understand what 'scale' is critical. Spawning studies are ongoing at UNH and at

SMAST. We also need to know more about what is driving spawning movement? The UNH study indicated that habitat may be a key factor, but it could also be environmental factors such as temperature, depth or currents. Tallack exemplified this point using a figure of crab migrations in the English Channel; males show ‘rambling’ random movements of relatively short distances while the females undertake a long-distance directed movement into the prevailing current which then carries the spawned larvae back inshore for settlement; it is possible that a similar strategy may be used by cod.

Tallack noted that scales appropriate in one location might not be appropriate in others. Looking at distance traveled within one year at large, the lowest mean distances traveled have been observed for fish in the inshore Gulf of Maine, while fish on Georges Bank and in the Bay of Fundy traveled further on average. Another way of looking at it is how many cod released in an area stay in that area; for the inshore Western Gulf of Maine the retention rate was high (~81%) while in Downeast Maine waters retention rate was <1% (though some of this may be explained by low groundfishing effort in this area).

To date these cod tagging data have been used to inform the assessment and management process during the 2008 GARM (e.g. stock exchange rates and gear selectivity on cod across its size range), and during the 2009 TRAC (exchange rates of cod between Eastern Georges Bank and the U.S. (western) side of Georges Bank). The data have also been examined for evidence of movement in and out of closed areas (though the study was not designed for this).

Tallack concluded by posing several parting thoughts/questions: How should we determine the appropriate resolution for fine scale management? Based on relative movement or exchange between areas? Size structure? Habitat usage? Traditional or contemporary spawning grounds? Relative residency? She then posed the question of whether we should even be thinking finer scale; based on the obvious movement of cod across management boundaries, should we be thinking about single stock management instead? She also made some recommendations about priority research areas, including pursuing additional analysis on data we have and additional tagging studies with more specific questions.

Q: On the subject of migration highways: do you have any idea of the percentage of intermixing between GOM, GB and SNE?

A: We have an idea, but the models are still being tweaked. I haven’t apportioned to general areas – it is mostly done at a management area scale right now, and it depends on the fish size you’re looking at; we’ve looked at sub-legal and legal size fish separately due to the different exploitation rates. There is 80-90% retention in 4x, so remaining 10-20% are moving in from other areas.

Q: Did you look at capture and release relative to spawning times?

A: We did, though our analyses hasn’t focused on spawning questions because we only found (and therefore tagged) ~1000 spawning fish, even though our tagging trips coincided with spawning times. The recaptures tell us more however, and from these data spawning appears to be protracted, occurring in every month of the year and throughout the region.

Steve Cadrin, NOAA Fisheries and School for Marine Science and Technology (SMAST), University of Massachusetts—Dartmouth
(Please see Extended Abstract, Appendix A)

What is the spatial frame of the things we're doing in fishery science and management? Some observations happen at a very fine scale, as do fishing events. On the other extreme, many large-scale processes make the most sense when we look at the entire population. We have stock sizes, statistical areas, closed areas, rolling closures. What is the appropriate scale to deal with these issues? There is guidance from the legal regime -- National Standards 1, 2 and 3. We can also look at history, since we aren't the only group of scientists to address the issue of scale. Fluctuations make the most sense when we define the right spatial scale.

So now we can move to scientific theory. General theoretical population structures include single large populations that have homogenous vital rates and are panmictic, meta-populations that include reproductively connected subpopulations, and reproductively isolated subpopulations (either allopatric, the more rare geographically separated subpopulations, or sympatric, spatially overlapping subpopulations).

Most groundfish species are managed as single U.S. or transboundary stocks, with their management units based on homogeneity of vital rates, extensive movements, or a data-poor default. These are regional stocks with contingents, and despite their genetic homogeneity they sometimes have cohesive behavioral groups. These contingent structures have importance consequences for population productivity, stability and resilience.

Meta-populations cover species like yellowtail flounder. No genetic differences have been found, and some diffusive connectivity among subpopulations exists. Sympatric subpopulations, like winter flounder, may have a genetically distinct estuarine structure but are then caught as one mixed unit. Production among these subpopulations varies, especially with those off Maine coast being severely depleted and those in the western Gulf of Maine being more productive. We're also seeing a shift from estuarine spawning habitats to marine spawning habitats.

Cod shows a dynamic sympatry. With cod, it is not only overlapping spawning groups, but then there is movement all over the place. Tagging studies suggest that the mechanism of reproductive isolation is natal homing to distinct spawning grounds or seasons (Ipswich Bay vs. Massachusetts Bay), though not on Georges Bank. There appears to be an annual return of recaptured fish to the place where they were spawning when tagged. Failure of productive spawning groups in the western Gulf of Maine to repopulate traditional cod habitat of eastern Maine suggests that spawning groups are not reproductively connected and adapted to distinct migration circuits. This explains why the stock assessment and fishermen disagreed about what was happening.

Other fishery resources that exhibit dynamic sympatry are effectively managed at multiple scales using stock composition analysis. Further work is needed to identify 'natural tags' to apply to stock composition analysis of cod off New

England (genetic characters, otolith microstructure or otolith chemistry). Using oxygen and carbon isotopes of otoliths, we can differentiate which fish spawned in winter, and which spawned in the spring. This can be used to test natal homing. Hopefully we can complement genetics with some of these natural tags. We can also use archival tags to increase out understanding of the environmental cues that initiate dispersive and homing behavior. This can help to develop an accurate view of cod's dynamic sympatry (including temperature and depth).

The science of stock identification involves determination of practical boundaries, heterogeneity and connectivity. Many aspects of groundfish ecology are manifest at small spatial scales, and finer scale management could benefit from local ecological knowledge of the resource. Many critical aspects of population dynamics occur at more regional scales. We may misinterpret patterns if we manage too finely, and we may fail to recognize important patterns if we manage at too large a scale.

Q: *In northern crest of the Gulf of Maine, there are no cod and no haddock. Tagging studies completed show that something else has changed. There are no fishermen there because there are no fish. The fact that local stocks aren't recovering is evidence that they are not panmictic, but rather local populations. I hope somebody jumps up and says I wonder why there's nothing there.*

A: This is why I think these issues make more sense at different spatial scales. It explains why fish subpopulations are repopulating depleted stocks, because they have different adaptations.

Martin Castonguay, Department of Fisheries and Oceans, Canada
(Please see Extended Abstract, Appendix A)

Dr. Castonguay began by addressing the reasons for using acoustic arrays. The technology is relatively low cost, and addresses some of the limitations of conventional tags. It is based on deployment of arrays in strategic locations plus acoustic tagging of fish. The low cost makes it feasible to tag large numbers of individuals to allow us to make inferences at the scale of the population.

Most receivers (i.e. Vemco VR2) have to be retrieved to obtain the data. Newer receivers (i.e. VR3 and VR4) resolve this problem by relying on modems, but battery life may continue to limit data obtainment. Another challenge is that tagging surgery requires reasonably good weather, as does retrieval of receivers. DFO has developed experience using acoustic arrays to shed light on cod stock mixing and stock structure issues over the course of three studies: 1) stock mixing between Gulf of St. Lawrence (GSL) and Sydney Bight (SB) cod; 2) Cabot Strait—stock mixing between Northern Gulf of Maine and southern Newfoundland cod; and 3) stock sub-structures in northern cod.

In the GSL/SB study, the fish migrated all over the array. Detection efficiency estimates allowed us to calculate the proportion of fish moving into the neighboring areas. In the Cabot Strait study, we found a distinct migratory corridor, and we also found that fish migrated into the neighboring management area in December and came back to their proper management area in April. The biggest pulse was during the last two weeks of the year. In the third study, we used telemetry to shed light on northern cod substructure. It involved more receiver arrays and surgically implanted transmitters. In this project, 30 moored arrays have been continuously monitored since 2006, with coverage expanding slightly between 2006 and 2008. Arrays were 500 meters from shore, and 0.8 km apart heading seaward. This allows for 100% receiver efficiency. How many fish tagged? Seasonal trends showed the fish leave the fjord in Smith Sound in summer, and nearly all return in the winter (Jan-March). This cycle was seen repeated over 3 years, and the proportion returning depleted over the three-year period, so you wonder if there is a link between this reality and the offshore repopulation event currently appearing (cod are currently undergoing rebuilding in the offshore).

Canada has not done any offshore tagging since the early 1990's, and the survey has not found any aggregations of large fish (i.e., > 60 cm). The situation is changing now, as a recent acoustic tagging trip found aggregations of larger cod. 147 fish were released with transmitters, but had been caught by a trawler so their post-release mortality was likely to be high. Tagging and telemetry indicated that a substantial portion of the offshore cod aggregation migrated inshore during summer, rendering them vulnerable to inshore fisheries (the exploitation rate of these offshore fish inshore is about 6%). Management of inshore and offshore as separate components is now inconsistent with new information on migration patterns.

Scale issues are probably not among the leading causes impeding recovery of groundfish stocks in the Gulf of Maine and Georges Bank. Appropriate scales for management may depend on abundance, as was seen in northern cod, and finer scale management may be more appropriate at depleted levels but inadequate when populations rebuild. It also may be appropriate during some seasons but inadequate at others. We need to spread fishing effort out to avoid overexploitation of local populations.

Q: *What does a 160 km array cost? What kind of lifespan/maintenance can we expect?*

A: A receiver roughly costs $2000, so with 60, about $120,000. You have to replace batteries and retrieve data at least once per year. New generations of receivers allow data retrieval through a modem but you still need to access the receiver to change batteries.

Adrienne Kovach, University of New Hampshire
(Please see Extended Abstract, Appendix A)

Dr. Kovach discussed some work on genetic insights into stock structure of cod in US waters. The classical view of marine species is one of high connectivity, high dispersal potential at all life stages, and barrier free environments. There has been a paradigm shift towards a finer scale, based on spawning site fidelity and natal homing, oceanographic features, egg and larval retention, local adaptation to environmental conditions, and potential for organisms in the same areas showing multiple life histories. Cod movements do not conform to the two stock management model we currently use. Kovach's research objectives included characterization of population genetic structure, determination of temporal stability, and assignation of juveniles to populations where they originated. Sampling sites included some spawning sites, some resting aggregations, and spring and winter spawning fish were separated.

This current work represents work from 2006-2008, expanding upon earlier findings with intention to characterize population genetic structure of cod in U.S. waters, including to identify additional spawning aggregates and determine temporal stability of structure, and assign juveniles caught on their nursery habitats to the populations from which they originated. We collected 1500 fish over two and a half years at a range of sampling sites from Bigelow Bight in coastal Maine, with red circles indicate spawning aggregations and blue indicating non-spawning aggregations, to Georges Bank and down to Nantucket Shoals, Cox's Ledge and New York Bight.

FST values describe how different populations are. In theory they range from 0 to 1, with 0 being identical and 1 being completely distinct. Fish tend to have small FST's, though you still can have statistical and biological significance with these small values. Primary differences come from the spring-spawning inshore Gulf of Maine populations. There are also big differences with Georges Bank and southern populations (Nantucket Shoals and Cox's Ledge populations). There are about 29 out of 45 possible comparisons are genetically different populations if you are less conservative in interpretation. Populations clustered are the most similar genetically; the three that cluster differently from the rest are the Massachusetts Bay spring, the Ipswich Bay spring and in Bigelow Bight, the main population in the spring. In previous work, Kovach found genetic heterogeneity within three inshore Gulf of Maine populations.

This simplified view of spawning complexes explains the biggest differences that are occurring. It shows three groups that are the most distinct from one another. Inshore Gulf of Maine overlaps with inshore winter populations and southern sites. Fish on Georges Bank are pretty different from southern fish and more similar to offshore Gulf of Maine than to inshore. We also see even finer structure than this and can test through a molecular analysis of variance (AMOVA). Between complexes showed there are very significant differences, but also among sites of some complexes there is also very significant differentiation.

There are many fine scale structuring mechanisms. Is there a genetic vs. plastic component to spawning time? Are there different strategies for residents vs. migrants? We've heard about fish being more sedentary in some areas, or more resident. Do we have natal homing or adoptive migrants after dispersal? Environmental forces in different seasons may affect dispersal, and there are historical population processes.

Typically in population genetic studies we use markers neutral to selection. However, we knew and demonstrated by our own selection tests, that two markers used in our study were impacted by selection. The ones that were affected by selection showed the biggest differences. What does that mean? We are not completely sure, as there is no consistent pattern.

To conclude, we did show a lot of fine scale spatial and temporal structure. We were able to assign juveniles to the complexes from which they originated, using a mixture modeling analysis. However, we could only do northern vs. southern complexes, not to specific spawning locations.

Q: Did you run your FST tests without the markers?

A: Yes, and they were too small to tell anything, so the neutral markers don't show a lot. Typically most studies use one two or three that are now pretty well known.

Panel: Potential Drivers of Stock Structure and Fine-Scale Movement

Bob Steneck, University of Maine
(Please see Extended Abstract, Appendix A)

Dr. Steneck begins by noting that one does not have to go back too far to find that the prevailing notion was that recruitment and local dynamics were driven by open marine populations. At the time, people were thinking if you knew how long larvae persists in the water column you could estimate dispersal distance from oceanographic information. Based on these simple models, it was commonly assumed that marine propagules (spores, larvae, etc) are widely dispersed, adults are more sedentary, and that marine populations were open and well connected due to long distance dispersal. Was this paradigm true? Biophysical models have become much more sophisticated, and the marine populations may actually be more closed than we thought. The field of connectivity has blossomed, and that's what we'll explore here.

When thinking about connectivity, you start with reproduction. This feeds into physical transport and larval behavior and survival, then larval settlement. The response of larvae to settlement cues is very important. These bits describe the pattern of dispersal, or the dispersal kernel. This is all under the larval connectivity umbrella, which is not the same as demographic or genetic connectivity. After settlement post-settlement survival to sexual maturity is important. Connecting those dotes includes adult migration and other things to add up connectivity.

At the end of the day, what is critical for management are the rates of recruitment, growth and survival that equal or exceed the local rates of mortality. That is what is known as "demographic connectivity". Demographic scale of connectivity determines things like population resilience sustainable harvests. However, many tools used to measure connectivity involve molecular genetics but this only measures the evolutionary tail of the dispersal kernel. The evolutionarily relevant portion of the dispersal kernel does not sustain populations, but it regulates gene flow and prevents species from going extinct. It can also be important to reseed locally extirpated stocks. If you have a genetic distinction, you absolutely have a break in demographic connectivity. When larvae were thought to be mostly passive planktonic particles, they direction and rates of movement were defined by simple advection. , The distance larvae could travel before settlement was much greater than is believed to be the case today. We know larvae have complex behaviors that result in greater self-recruitment than anyone thought was possible. For example, are planktonic, others very active swimmers, but they also influence retention of dispersal through mechanisms like buoyancy. If you have no behavior or oceanographic eddies, they might go 50 kilometers over 30 days but the distance may shrink when you add larval behavior or oceanographic factors. All of this points to the incredible shrinking dispersal kernel.

Many fish recruit very locally. But this is not just a larval dispersal story. There are many recruitment bottlenecks. High larval connectivity can result in a huge number of larvae arriving to a site but if the nursery habitat is not receptive to these larvae, high levels of settlement and post settlement mortality will result in possibly no surviving recruits. Whatever contributes to post-settlement mortality resulting in few or no individuals surviving to sexual maturity means demographic connectivity is severed and the populations cannot grow or sustain themselves. We should think about this in a cradle to grave way. We hear a lot about SSB and we think a lot about stock recruitment relationships, but in between those we have all of these other factors related to dispersal the habitat and their reproductive success. We need to determine what explains the most variance in demography. You can look at this with respect to capacity of stocks to migrate and their population size. So if you have a large pop size and high migratory ability, it might be functioning more like an open population, but if you have a smaller population with limited migration, it could be a closed population.

These things are probably dynamic over time. You may have had functioning meta-populations in prehistoric times, but now they are a dysfunctional network. That is, the stepping stones between local populations that allow their maintenance are no longer there because we have seen stock depletion over time. In conclusion, we need to get at larval connectivity, demographic connectivity and genetic connectivity. The changing paradigm is that marine populations may be more closed than previously thought. Demographic connective differs from genetic connectivity and operates at smaller scale. Relatively closed meta-populations may be highly dynamic and may have changed over time and uncertainty remains. Studying this problem at a finer scale is warranted and may be a better plan for management. It also makes sense to think of the system at finer scales that can be combined to build a larger picture. This would be easier that starting with populations at large scales and trying to discern the finer scale from that.

Q: *Can you explain how the absence of settlement cues depresses recruitment in a region?*

A: Regional cues trigger a developmental sequence that translates to a behavioral sequence that makes larval fish move to nursery habitat. Some cues are known to trigger early metamorphosis in fish improving their ability to swim to nursery habitats. Sounds can cause this, and there have been suggestions that long distance larval swimming may be important for lobsters, but I don’t know of any directly applicable to groundfish in the Gulf of Maine.

Q: *If we accept premise that codfish, pollock and haddock are trying to return to historical spawning grounds, do we explain redfish by using term chaotic system term and why are they different from the other three species?*

A: Redfish form my perspective, seem to occupy diff habitats from cod and haddock, more centrally distributed in the Gulf of Maine instead of peripherally. Also, Steve Murawski mentioned the characteristics of depletion because it sounds as though, if they were spatially depleted, they must have been locally recruiting or you would anticipate depletion in one area would bring all stocks down.

David Townsend, University of Maine

Demersal fish are found on continental shelves in temperate latitudes because those areas are productive with big spring plankton blooms. That is the big scale. Smaller scales address life history stages that are dependent on sub-regional patterns of productivity. As early as January the spring phytoplankton bloom is underway in the inshore Gulf of Maine and on Georges Bank. This is because phytoplankton are dependent on light, and vertical mixing is insufficient in deeper waters, so the bloom happens inshore in shallower waters. In 2006, like most years, the spring bloom began off Nova Scotia because around Nova Scotia comes a surface water layer that is cold and fresh and is already stratified, then it shows up on Georges Bank and over to Jordan Basin and into the Gulf of Maine, then spreads into the western Gulf of Maine. This phenomenon is known to deliver as much as 50% of the organic matter to the benthos. These big stocks of fish eat things on the bottom, so the benthic food web is driven by spring bloom of plankton.

After the bloom, we see some smaller scale patterns emerge. Small-scale productivity depends on the source of nutrients, where they go and how they mix upward. Penetration of deep slope water is the source of salt and nutrients to the Gulf of Maine. Tidal mixing of that cold water happens in a process called tidal pumping and nutrients come to the surface here, circulate and move around. This produces the eastern Maine coastal current, and the nitrate levels drop down because phytoplankton are taking it up. Copepods are propagating in response to this pulse, which makes the phytoplankton levels drop off. So nutrients are in the eastern Gulf of Maine, phytoplankton further along the current, and zooplankton down in the western Gulf of Maine, on average, because of this feature.

On Georges Bank it's even more interesting. The coastline goes around on itself. The nutrients come onto the bank from Franklin Basin, enter a vigorous circulation on the bank where the highest biomass of phytoplankton exist, and zooplankton propagate, and fish tend to spawn here because of it. I left out estuaries and embayments. They are important—enough said.

But the whole system is changing. Based on historical stations going back 50 years, we put together all the nutrient data available because we wanted to see what was coming in at depths over 100 meters to see what has been coming into the GOM at depth. We took a 50-year average of temperature, salinity, silicate, nitrate, and plotted the anomaly. If you look at how the nutrients change, in the 1960's we had low nitrate levels, and in the 1970's nitrate went way up and dropped off. Silicate went way up and stayed up. We became suspicious that something was going on based on survey cruises we did in 2005 when the silicate levels were higher than nitrate levels, which has never been seen before. In the 1960's, the silicate exceeded nitrate as well. From our analysis, we believe that diatoms interfere with large dinoflagellates, and after the diatom bloom, when nitrate and silicate levels are drawn down, there is still enough nitrate leftover, which is all the dinoflagellates need.

The 1960's were the heyday of groundfish. When you get red tides, they tend to preclude the second phytoplankton bloom that usually happens on Georges Bank. When silicate levels go up, nitrate levels go down over time. What is causing this? If Labrador slope water or warm slope water are the source waters, how can there be more silicate in the Gulf of Maine when these waters always have more nitrate than silicate? The general consensus is that our nutrients come through the Northeast Channel, which is 220 meters. But what if we're now getting water across the Scotian Shelf? There is also a channel between southwest Scotian Shelf and Browns Bank that is deeper than 150 meters. In this large scale circulation, if the Arctic is melting it would intensify this buoyancy-driven current, which is the inner arm of the Labrador Current. The Labrador slope water usually comes down through the Northeast Channel. What if that water current is now moving along the Scotian Shelf, undergoing denitrification as it travels over the shallow continental shelf, thus reducing nitrate level and potentially concentrating silicate?

Dr. Townsend predicts that we are heading into a phase (not driven by the North Atlantic Oscillation) where the Gulf of Maine deep water is getting colder and fresher, which is favoring diatom production and groundfish production, and working against red tides.

Q: Can you talk about travel time for that water?

A: A couple of years.

Q: I think we've seen a freshening of waters in Labrador current, have you seen it in Gulf of Maine?

A: Yes, but we have also seen freshening and salting in multi-decadal cycling so it is not clear if it is part of that cycling or not. The North Atlantic Oscillation should mean we are getting more Labrador Slope water, but instead we are seeing the reverse.

James Churchill, Woods Hole Oceanographic Institution
(Please see Extended Abstract, Appendix A)

Dr. Churchill began by referencing data from the National Marine Fisheries Service spring surveys of 2000-2005, which show a number of population centers of cod. His focus is on the concentration of cod found in the western Gulf of Maine. He noted that, based on recent tagging studies, this population appears to be sedentary, tending to remain within the western Gulf of Maine. Furthermore, recent work (summarized earlier in the meeting by Adrienne Kovach) reveals that the spring spawners of this population are the most genetically distinct of all cod spawning groups in the Gulf of Maine.

Churchill's research seeks to address some fundamental questions regarding the cod population in the western Gulf of Maine. Of principal concern to managers is an understanding of what controls the variations in recruitment success to this population. Even though NMFS surveys have persistently found high densities of cod in the western Gulf of Maine, the recruitment success of these cod has exhibited considerable variation. Churchill's work seeks to understand what controls this variation in recruitment success, and to what extent it is related to variation in the regional circulation. Of more fundamental scientific interest, Churchill's research seeks to better understand how the western Gulf of Maine cod stock has evolved and is maintained.

In addressing these issues, Churchill's approach has been to use circulations fields generated by numerical models to simulate the movement of cod larvae spawned in the western Gulf of Maine and determine the probability that they can successfully reach areas in the western gulf suitable for early-stage settlement.

The focus has been on cod spawned in Ipswich Bay during spring. The spring spawning (typically in May and June) is one of two major spawning events that occur in the western Gulf of Maine. The other takes place in winter (roughly from Dec.-Feb.) at locations in both Ipswich and Massachusetts Bays.

The cod spawned in these events may become exposed to the larger Gulf of Maine circulation. In the western Gulf of Maine, this takes the form of two along-shore currents. One is the Western Maine Coastal Current. Its name is somewhat of a misnomer, as it does not flow adjacent to the coast, but is typically centered between the 50 and 100-m isobaths. The other is the Gulf of Maine Coastal Plume, which is forced by the accumulation of fresh water from river discharge, and appears to be weaker and more ephemeral than the Western Maine Coastal Current.

In determining the likelihood that the spawned cod may reach areas suitable for early stage settlement, developing eggs were released into the modeled flow field from the Ipswich Bay spawning region. For each release, the eggs were distributed evenly over the spawning region, the boundaries of which were specified based on observations of fishermen and researchers. Releases were done every three days throughout the spring spawning season (May-June).

In tracking the cod within the modeled flow fields, the developing eggs were assumed to be buoyant and reside near the surface. After 20-days of development, the cod larvae were assumed to be capable of daily migration in the water column, moving to deep water during the day to avoid predation and rising to the surface at night for feeding.

The probability that the spawned cod may reach an area suitable for settlement in the western Gulf of Maine, denoted as the transport success, was taken as the likelihood that the eggs/larvae released from the Ipswich Bay spawning region be over an area suitable for settlement at an age when they are settlement capable (nominally 45-60 days after spawning). Based on the distribution of age-0 cod, determined by Arnold Howe and others of Massachusetts Division of Marine Fisheries, the habitat suitable for early-stage juvenile cod settlement in the western Gulf of Maine was taken as areas with depths shallower than 30 meters. The estimate of transport success may be taken as an indication of the effect that ocean currents have on the overall recruitment success. Transport success estimates were computed for the spawning seasons of 1995-2005, years for which model flow fields (supplied by the Marine Ecosystem Dynamics Modeling Lab of the University of Massachusetts at Dartmouth) were available.

A principal finding was that the variation in transport success was strongly related to wind direction. Specifically, the transport success varied depending on whether the local wind was upwelling or downwelling favorable. For example, the transport success for those larvae released in May tended to be high for those years when the mean May wind was downwelling favorable. The reason for this is relatively simple. When the wind is upwelling favorable, buoyant eggs released from Ipswich Bay will tend to be carried offshore by the upwelling circulation. If this circulation persists long enough, the eggs will be carried to the Western Maine Coastal Current, which will transport them rapidly out of the Gulf of Maine. By contrast, a downwelling circulation will tend to carry buoyant eggs onshore and keep them within the western gulf.

This mechanism is also responsible for a difference between the transport success estimates of the May and June releases. For all years, the transport success of the May releases is higher than that of the June releases. This is the result of a shift in the mean wind direction in the western Gulf of Maine going from May to June. The mean winds of June are always strongly upwelling favorable, resulting in a circulation that tends to carry the buoyant eggs from the Ipswich Bay spawning area into the Western Maine Coastal Current.

Transport success was found to be fairly well correlated with recruitment success. This leads to the hypothesis that the mean wind in May may be a good indicator for recruitment success. That is, cod recruitment to the western Gulf of Maine may tend to be highest for those years when local winds are predominantly downwelling favorable during May. Comparing the full suit of recruitment success estimates for the Gulf of Maine (which date back to 1984) with the mean May winds over the western gulf indicates that this is indeed the case. The years with the highest recruitment success are also the years with the most strongly downwelling favorable winds during May. This trend is nicely exemplified by the May winds and the recruitment success estimate of 2005. The recruitment success for Gulf of Maine cod was the highest on record in 2005, and the mean wind stress of May 2005 was the most strongly downwelling favorable mean May wind for the 22-year period over which recruitment success has been estimated.

Modeling was also done to track the movement of cod spawned in Ipswich Bay during the winter. Tracking cod eggs in the winter is somewhat problematic because of uncertainty of their position in the water column. During the spring spawning period, the water column tends to be strongly stratified, making it reasonable to assume that buoyant cod eggs will be maintained in the near-surface mixed layer. However, during winter, the water column is vertically mixed, making it difficult to ascribe a depth range over which cod eggs are likely to be found. This caveat must be kept in mind when considering the modeled tracks of winter-spawned cod. Nonetheless, it's worth noting that these tracks indicate that winter-spawned cod eggs maintained near the surface will tend to be rapidly transported out of the western Gulf of Maine. This is the result of the strong upwelling-favorable winds prevalent during the winter spawning period, which induces a circulation carrying buoyant eggs spawned in Ipswich Bay offshore to the Western Maine Coastal Current.

Churchill ended his talk by offering three hypotheses on the spawning and recruitment of the western Maine cod population. One is that this population may carry out something of a two-spawning strategy. As suggested by the analysis reviewed above, the spring spawning may principally supply recruits to the local, sedentary-resident population in Ipswich and Massachusetts Bays. By contrast, the larvae produced by the winter spawning may tend to be carried father afield and nourish more remote populations. This dual-purpose strategy may, over time, serve to sustain the local, western Gulf of Maine, population as well as the larger-scale regional population of cod. This hypothesis is consistent with analysis of genetic markers that Dr. Kovach presented in an earlier talk. Her work indicates that spawning cod found in Ipswich Bay during spring tend to be genetically distinct from other regional spawning assemblages, but are genetically related to the juvenile cod found in Massachusetts Bay. By contrast, the spawning cod sampled in Massachusetts and Ipswich Bays in winter tend to be genetically related to other regional cod assemblages.

The second hypothesis offers a possible reason as to why a concentrated population of sedentary-resident cod is found in Massachusetts and Ipswich Bays, while cod populations elsewhere in the Gulf of Maine have become decimated. Churchill noted that these bays form the only large area within the coastal Gulf of Maine that is not exposed to the Gulf of Maine Coastal Current. The bays may be viewed as something of a "pocket" where retention of locally spawned cod may be most possible. Furthermore, the spring spawning of cod may be concentrated in Ipswich Bay, at the upstream end of this "pocket", because this is the area of egg release where subsequent retention within the bays is most favorable.

The third hypothesis conjectures that the spring spawning event in Ipswich Bay might have evolved over time precisely because it occurs at a time of year and at a location for which released cod eggs are most likely to be retained in the western Gulf of Maine.

Churchill noted that part his future modeling effort will be directed at testing these hypotheses.

Q: Does timing of tidal currents and vertical migration impact this at all?

A: Tidal ellipses in Ipswich Bay are relatively small, so timing of egg release in tidal cycle doesn't seem to have much impact on the subsequent transport of the eggs.

Q: In the past, we had significant cod much further to the east. Using your logic, do you see arguments for the sustainability of the eastern stocks?

A: Because of the influence of the Gulf of Maine Coastal Current, it's possible that there would not be local recruitment for those stocks. It's also possible that these stocks may have partially sustained by delivery of larvae from an upstream population.

Q: Why don't larvae transported offshore survive?

A: They may survive but I wasn't considering those in the present study, which was focused on self-recruitment in the western Gulf of Maine. However, I have looked at connection between larvae spawned in Ipswich Bay with Georges Bank and Nantucket Shoals.

Jonathan Grabowski, Gulf of Maine Research Institute

Dr. Grabowski began by recognizing that he spends a great deal of time thinking about how habitat affects fish populations. While the studies are often small and focused, the idea is to extrapolate to larger scales and population structure. He began by looking at the literature and scaling out. Past work has indicated that substrate type affects less than one percent of the variation from the trawl survey data, as opposed to bottom depth or temperature. This was sobering for someone who works on habitat at large scales.

That work also says that temperate fish are extremely mobile and we need to be careful about applying lessons from reef fish because they're very sedentary as adults, generally and those strong habitat associations don't necessarily exist for Gulf of Maine species. However, the authors pointed out that assemblage level analyses may obscure size and age class linkages to benthic habitat features, which explains the disconnect between larger scale findings like this and the work Grabowski would discuss later. And they did find that cod actually show a slight preference for coarser habitats. It's unclear if particular habitats have a disproportionate effect on vital populations. We want to know what the linkages are between Essential Fish Habitat and the growth and mortality of fish so that we can enhance management of these important species.

Some of the linkages we do see with fish species and habitats are that juvenile cod are predominantly in shallower habitats in the coastal portion of GOM. Seagrass beds, kelp forests and probably even ledge habitat can be very important for juvenile cod. Most of these studies are very small scale and we've seen compelling demonstrations of how habitat functions as refuge habitat when there are juvenile cod predators around. Larger juvenile cod (1-2 years) seem to prefer rocky habitat and gravel habitat to sand and mud. So is habitat limiting groundfish biomass in the Gulf of Maine? This is a critical question we should be asking.

We do see some examples of fine scale structure within this heavily exploited species. So how do we remedy the disconnect between this nice body of fine scale work and the large scale of stock structure, which is much beyond the scale of most experimental work? There are spatial and temporal patterns. We can imagine that if we have a species that exists across this range, through time it might subdivide into stocks. Habitat can drive this because it can play a role as a corridor that allows fish to move throughout the range. As corridors are lost through natural processes, you might have division of habitat, and subsequently division of subpopulations or stocks.

More generally, habitat, or habitat patchiness, can drive whether these population structures subdivide because of corridor effects, natal and spawning site fidelity, and natural or anthropogenic changes in habitat patchiness. As you get fewer and fewer suitable patches, you might see species separating along that oceanographic break. As a caveat, some past work has shown that proportion of sites with cod was positively correlated with the abundance of cod. In low recruitment years, primary habitats are occupied quickly, and those are eelgrass sites. When abundance was high, you found cod on unstructured bottom at decent abundances. So the idea that they are tied to highly structured habitats might not be entirely true, and habitat use might be largely driven by density-dependent processes. By evolving multiple discrete spawning periods throughout the year, a species may be reducing competition for resources during early life-history stages, which consequently could increase fish productivity.

In coastal Maine, we separated out the trawl survey data to analyze for young-of-year (YOY) cod found in fall vs. spring, and they were occupying very different habitats. YOY cod were more common in mud and gravel in fall, but dominant in the sand habitat in spring. That is driven by not just habitat but also by depth, because sand habitats were common at the shallowest depths, whereas mud were located at the deepest depths in this study.

On Cashes Ledge, we have looked at red and white-bellied cod. We have found high abundances of red cod higher up on the ledge, and reduced abundances of red cod at deeper depths, whereas the reverse is true of white-belly cod. They are not just different colors—we have lots of reasons for thinking they're two different eco-types. In addition to their dissimilar color and depth-ranges, they eat slightly different diets, have different shapes, and exhibit disparate parasite loads.

To come back to Ipswich Bay, there might be selection for different habitats if the time at which spawning occurs results in different dispersal patterns. So in conclusion, habitat can be an important driver of population structure, of course, but our understanding of that driver is limited for many key groundfish species. It is even more unclear the degree to which habitat limits adult biomass. Timing and location of spawning events is non-random. To what degree fish have formed spawning strategies to exploit critical habitat? And can we tease this apart from the few remaining unexploited (if any) and exploited populations? At what scales are these processes occurring relative to habitat?

Q: *When studying the body shapes of cod – do you consider whether they're ripe, spawning or spent?*

A: Yes.

Q: *A blight on eelgrass in the 1940's wiped out extensive beds. Do you have any comparisons of that earlier abundance of cod vis-à-vis eelgrass beds that exist today?*

A: Unfortunately we do not have adequate data on the extent of eelgrass or the abundance of cod from the 1940's.

Q: *In the Downeast coast where there are low amounts of fish populations, I was wondering about estuaries and marshlands. Would that affect populations in those areas, especially where there aren't many fish in the areas?*

A: Yes, it certainly could. When rivers such as the Penobscot are restored, we should be investigating whether marine species (in addition to anadromous species) that used to come into those estuaries recover.

Graham Sherwood, Gulf of Maine Research Institute

Dr. Sherwood focused his presentation on the adult life stage in cod. In particular, what makes adult cod stay home near natal habitats and what makes them roam? His introduction outlined five major areas of discussion: 1) First, to establish that movement is highly variable among groups of cod; 2) to ask what do we think drives movement variability in cod? 3) to introduce the concept of partial migration as a potential model for understanding movement variability in fish in general; 3) to provide evidence for partial migration in Newfoundland cod in relation to feeding and reproduction; and 5) to ask the question whether we are selecting for more sedentary cod through fishing practices and management in the Gulf of Maine (i.e. via closed areas).

Movement behavior is highly variable in cod. Dr. Sherwood began by referring to past work on historical movements of cod groups throughout the north Atlantic (Robichaud & Rose, 2004). In this analysis, we see a fair number of sedentary groups but the majority are considered migrant. There are also some east-west differences, with more resident cod in the northeast Atlantic. Interestingly, Robichaud & Rose (2004) also linked this variability in movement to other parameters of stock performance. Sedentary groups never really got very abundant, and the historically abundant groups were migrant fish to some degree, which led to the conclusion that “migration and dispersal beget abundance”.

But why? What drives migration in cod? It likely involves foraging and indeed Dr. Sherwood showed that there exists a nice relationship between capelin (a migratory prey fish) availability in Newfoundland waters and cod liver index, an indicator of overall condition and health in cod (Rose & O’Driscoll 2002). In turn, the liver index correlates well to things like the ability to migrate, reproduce, grow, etc. So there is an energetic advantage to going after this mobile prey.

Why then wouldn’t all cod migrate? Why be resident? Here, Dr. Sherwood turned our attention to how migratory behavior can vary not only among populations of fish but also within populations where some individuals are migrant and some are resident. In fact, this phenomenon known as partial migration is much more common in fish than we realize. And there are tradeoffs, which can explain this dichotomy. Looking at brook trout as an example, migrants (ocean-going individuals) have high growth (note: slide is backwards), which translates to high fecundity, but also high mortality (because of more predator encounters when they migrate out of the stream). Stream residents, on the other hand, have lower growth, lower fecundity but also lower mortality, since there should be fewer predators in the stream. So this tradeoff or balance allows the whole system to persist over time, theoretically. Differences also seem to manifest early in life before migration; migrants and residents have similar growth rates during the first year of life when they both coexist in the stream, although by the second year, migrant growth is much slower despite having higher consumption rates (Morinville & Rasmussen 2003). As a result, resident brook trout are twice as efficient as migrant brook trout. Thus, residents are more efficient and may be better able to weather ups and downs in resource availability, but migrants, being gluttons, may benefit from huge payoffs as long as they encounter abundant food.

A major lesson learned from studies of partial migration in fish is that we need environmental heterogeneity to drive this system. With brook trout, you have the difference between the environment in the stream and the ocean to drive major differences in energetics. The question then becomes, can you have partial migration in an open ocean system where this heterogeneity might not be as obvious? Dr. Sherwood then turned his attention to work in Newfoundland where as a postdoc he looked at food web variability and potential relation to recovery of cod, and where another student (Matt Windle) was doing homing experiments in Placentia Bay. Fishermen in Placentia Bay have said that fish seem to come into the bay to spawn in spring and leave after spawning, but that there also seems to be a resident population that sticks around after spawning. Dr. Sherwood decided to apply a stable isotope method for inferring past feeding habits in fish to tease apart whether reported residents have different foraging strategies (e.g., benthic versus pelagic) than the migrant cod that leave after spawning (presumably to go after capelin).

A total of 50 cod were tagged with acoustic “pingers” and followed by boat-based telemetry for a year. A small tissue sample was also taken from these tagged cod to compare movements with past feeding histories. Interestingly, the cod sampled showed the full range of feeding habits (via stable isotopes) as that seen throughout all of Newfoundland; i.e., some were very pelagic and others were very benthic. As expected, pelagic cod took off after spawning and benthic cod stayed closer to the spawning site. In addition there was a higher degree of homing for benthic (resident) cod, which makes sense since they should have had less distance to travel for return. From other cod lethally sampled at the same site and time as the tagged cod, a pattern was seen where benthic fish mature earlier and invest more energy in reproduction up front compared to the pelagic cod, which reserved their reproductive effort for later in life. Dr. Sherwood mentioned that this gets back to the energetics argument—that residents (benthic cod) are living in a limited system that supports growth at earlier stages but as they get older there is a poorer return on a poor diet and hence, they ‘cash in their chips early’. Migrant fish, on the other hand, can probably get returns on effort later in life as far as reproduction, so they follow more typical body size fecundity relationships (i.e. fecundity continues to increase with size).

There are interesting implications of this finding. A recent paper in Nature (Olssen et al. 2004) has concluded that fishing induced selection has resulted in early maturing fish within the Newfoundland population. Dr. Sherwood argued that his results suggest that the same pattern of decreased age at maturity could have been produced by selective removal of one type of cod (i.e., the later maturing migrants). Consistent with this, offshore migrants were probably more vulnerable to the offshore fishery than the inshore residents. So this becomes not just a question of maturity, but also selection for difference in movement behavior and other life-history traits (e.g. diet and growth).

Finally, Dr. Sherwood turned his attention to cod life-history questions in the Gulf of Maine and how management may be affecting the relative frequency of types.

In particular, there is a large amount of bottom permanently closed to fishing in the Gulf of Maine and on Georges Bank. Given that we know that cod may exist as resident and migrant forms, the question arises; do closed areas favor resident cod that may stay within closed areas boundaries? There is reason to believe that closed areas favor resident types of fish. For example, haddock (a more sedentary gadid species) seem to respond particularly well to closed areas. To highlight this, Dr. Sherwood showed results of another study where he set up an array of acoustic receivers in the northwest corner of Closed Area I to monitor residency behavior of acoustically tagged haddock. Results of this study pointed to a high degree of residency for tagged haddock within the closed area and even were suggestive of an active "choice" by some haddock not to leave the area.

Getting back to the question of whether closed areas are having an impact on cod life-history variation (and by corollary favoring one type over another), Dr. Sherwood presented some preliminary results of a comparison of cod captured inside and outside of closed areas. Morphometric (body shape) analyses revealed that cod inside of closed areas have more robust body shapes than cod outside of closed areas. In fact, the cod inside closed areas have body shapes more similar to red cod, which are suspected residents (Sherwood & Grabowski are also exploring life-history differences among red cod and normal cod). The body shape analysis may also be helpful for inferring stock structure. From Dr. Tallack's presentation, we saw an exchange between the western Gulf of Maine and western Georges Bank, which seems to be a mixing area. The fact that body shape is similar between those areas but not others is consistent with the tagging data. Body shape has been used historically for stock distinction, so this suggests that we might want to go back to using this as another discriminating variable in our analyses.

In conclusion, movement is highly variable among and within cod populations, and variation appears to be driven by environmental heterogeneity (pelagic vs. benthic prey) as well as specialization in life-history strategies to take advantage of different aspects of the ecosystem. Residents are generally less productive than migrants. Closed areas may be favoring residents, and contemporary movement studies may be dealing with an altered state, with more local stocks.

Q: *Regarding the fish on Cashes Ledge that you think are sedentary--are they also spawning there?*

A: The ones we sampled were not in a reproductive state but we think they are, yes. We are trying to get out there and hopefully encounter some spawning fish there. They are always on top of the ledge in shallow waters so we think they are very local and resident and we want to see if they have other characteristics that would demonstrate that.

Q: *Are you suggesting that the two lifestyles are hereditary traits?*

A: Good question. In trout, they are. If you put a barrier to migration, then you lose the migrant genes.

Q: *Do you have evidence of timing of spawning, which fish become resident, and which become migratory? Is it reset every year?*

A: I'm not sure, but if it is not genetically determined, it might be based on divergence at early life history stages based on environment. For trout its been shown but for cod we don't know. It seems from other talks that early spawners are more adapted to this large-scale dispersal whereas later spawners seem to be retained and they may be developing into sedentary types. So it might be genetic or maybe you just end up in the right habitat at the right time of year and settle into that lifestyle.

Q: You talked about migrant vs. resident and early onset of maturity for resident cod. Is there evidence of higher mortality for migrant vs. resident cod?

A: We think they are not necessarily dying, but their growth is stunted.

Discussion:

Q: Where are critical juvenile habitats in Gulf of Maine, and how important are they in total life history for cod and other species? Are there any major ones?

Responses:

- If you look at NMFS trawl survey data, there are distinct aggregations (Mass Bay, Great South Channel, eastern Georges Bank). Except for the young of the year, I don't think we have the habitat information to map out the specific habitats.
- Dr. Grabowski's work showed juvenile habitat to be best in rocky bottom, but aren't the best concentrations in sand bottom?
- Trawl survey data can't sample really hard habitats.
- This is a challenge as we continue to use trawl surveys, which aren't very efficient in highly structured habitats. It will be a priority to get onto Nantucket Shoals and the top of Georges Bank. We should be using more and different sampling methods.
- There is a strong correlation between hard substrates and juvenile habitat and this was trawl data. It would be beneficial if we could add substrate as another data point to the trawl survey.
- There is beautiful nursery habitat on the eastern Maine coastal shelf.

Q: *Has there been any work done to define the mortality rates from predator species? Then we'd know more about natural mortality for management efforts.*

Responses:

- People who study Baltic cod think that what has happened there is that sprat, which are cod prey, have grown. So sprat were feeding on cod larvae. We've thought about herring feeding on cod eggs, but what about seals? They're more abundant in the Gulf of Maine than before, and may be eating juvenile cod. The same could be true for alewives and river herring. The ecosystem may just be fundamentally different.
- The largest portion of young of year cod is in the Nantucket Shoals area and there's a proposal for a new closed area with the objective of protecting juveniles

south of Cape Cod. The area was sampled using hook gear so that would have different impacts than trawl gear.

Q: *Is it possible to say how much population richness or genetic variability we've lost over the years? How does it compare before trawling was widely occurring?*

Responses:

- This is simple if you have archived otiliths, etc. It has not been done in this system, except for one Canadian project about 6-7 years ago in one population.
- There are a series of haddock samples that could be used.

Q: *I am thinking about gaps in knowledge—what is happening in the eastern Gulf of Maine? Something is obviously different than the western Gulf of Maine. Lots of tools have bee discussed today. How might we determine how that system might have once worked and what might bring it back with different oceanographic variables? Maybe we should not look where fish are, but at the area to find out why they aren't there.*

Responses:

- Maybe as regards baseline population structure and richness, we manage fisheries as opposed to fish. While a great deal of productivity was observed in the past, that productivity was driven by a different population structure. Should we dampen our expectations?
- If we want groundfish to rebound, don't we have to look at the system holistically and make sure that we feed fish correctly? If we remove too many prey species, like herring, what impact does that have?
- One fisherman we work with thinks seals disrupt spawning. Maybe cod that used to spawn inshore are now spawning offshore because seals are chasing them.
- We have a wealth of studies that speak to population structure that did exist for cod – that is really valuable. Even if two populations don't show genetic distinction, they should be managed differently. Genetic differences show the extreme of distinction. That tool should be used with other tools – such as otolith microchemistry.
- We've not talked about other groundfish today. We should repeat all of these studies and look at other species as well.
- Depletion doesn't necessarily mean a loss of species population richness. Life history changes in relation to environmental changes and other forces.
- We should also put out a life history timeline and try to see where we have good information. Where is there evidence for demographic factors at work and why? What are the demographic bottlenecks? We could then go after a strong research strategy quite surgically.
- Fishing seems to be affecting size structure, so you start selecting for a number of life history traits. This may be forcing populations to track fluctuations in environmental conditions. Populations of small fish may be less equipped to handle these shifts than larger populations of fish.

Q: There's also a shift towards ecosystem-based management as well as finer scale…can we resolve these two scales? Ecosystem-based management may be considering the larger system and we're talking about substructure. Are these two concepts mutually exclusive?

Responses:

- Management strategy evaluation may be a new tool that could help answer that question. Australia uses a full ecosystem model and then generates simulated landings data and survey data so they can test whether appropriate spatial management scale is appropriate for the ecosystem scale. This is almost as squishy as ecosystem-based management but may be part of the answer.
- We'll be forced to work at multiple scales. Some migratory fish operate over very large scales but prey may be managed at smaller scales. We need to think about interaction between benefits for sedentary species in closed areas and larger more migratory species that simply move through them, and what's going on in closed areas at a much different scale?
- Just to reinforce the point, I am hesitant to pick a scale, I think we need to work with a hierarchical paradigm because many are climatic, and many are local. There are connections both ways. We need to take advantage of meta-analyses-- how populations decline and history as they've increased. Generally they're asymmetrical and that can help us understand the requirements for successful populations. We talked a lot about why populations shouldn't recover but we've had some of the best recoveries in our area (e.g. herring and haddock on Georges Bank, striped bass, scallops).
- If we don't go to multiple scales we'll induce serial depletion or we'll create intercept fisheries because we will create perverse incentives. It is important to figure out institutions that allow us to manage effectively from the social science realm.
- It is a tricky proposition to determine the appropriate scale at which to work. I've seen large bays near river systems that were incredibly productive and had predator species because of the enormous number of herring, plus spawning Atlantic herring. This created an enormous forage base and there's a synergy here. We need information about additional species to see if there is a core distribution pattern in these very productive systems.
- If you look at the body of work of Hall-Arber, Ames, Wilson and Hartley, it's socio-economics. I think we need to look at these issues on a small scale with socio-economic questions being asked and answered to manage the biggest predator we can control to get our fish back, and that's the fishermen.
- Issue of scale is overwhelming but I think Steneck gave us an excellent framework to look at study design.

<u>Panel: Different Perspectives on Spatial Patterns of Stocks</u>

Jim Wilson, University of Maine

Dr. Jim Wilson began by introducing the panel, which would respond to the panels and discussions from the day prior, and illuminate the fishermen's perspective on questions of scale. The panel began with a review of fishing community movement patterns by Dr. Madeleine Hall-Arber.

Madeleine Hall-Arber, Massachusetts Institute of Technology

Dr. Kevin St. Martin and Dr. Hall-Arber traveled to fishing communities, the impacts on which have to be considered in the course of fisheries management, to ask questions that bear on what constitutes a community—where people fish, their homeport, size of their crew, intensity of use, etc. Communities aren't just the homeport; they can be a gear group or some other connection between people. The initial reaction from the industry was they were being asked for proprietary information about where they fishes and were concerned it would be used against them. However, there were several factors that encouraged them to identify areas of traditional fishing uses to establish access rights to those locations, such as the Cape Wind project, and the Stellwagen Bank sanctuary. We worked with community researchers who interviewed key people in communities. The interviews were not random because some people know more about certain information needs than others.

Interviews were open-ended. Nobody had to answer every question or answer them in the same order. All interviews were recorded and most interviews have been transcribed. We asked people were they fish by gear group and different homeports and size vessels. Pink areas show higher intensity, with white areas being the highest intensity of fishing. We then took charts out to the communities to ground-truth what we had mapped. We asked a broader group of people if these areas were accurate. In most cases, homeport and primary port of landing was fairly agreed upon, but some people told us that we could not assume that if there was no cluster that an area was not actively fished. There were also changes as we were doing the interviews when some Portland boats started moving to Gloucester so they could land lobsters.

This shows who fishes in each location. Each port has a color-coded dot, and the circles correlate by color to the dots, showing where fishermen from that port tend to fish. We were asking people to define their fishing community, to see if they fished different areas based on the port they come from. Most will tell you they do not share information among other fishermen, but most were willing to share information with us, especially about weather and other safety issues. They also shared a lot of information about where to fish and regulations. If they were part of same community and fighting the same regulations they were more willing to share. We were not asking people to give us their hotspots—we were asking them to tell us where their peer group fished to get a picture of their community. People had a lot to say about where they fished that was not reflected by the clusters we identified.

Even with fine scale differences in where people fished, there may be huge differences in the catch. We also learned a lot about seasonal differences, impact of wind direction, etc. Many of the fishermen we interviewed were knowledgeable about these things and would be helpful to scientists in this way. If communities extend beyond boundaries of their ports, impacts likely go beyond those geographic boundaries. This is an important thing to think about.

Q: *Where is this data available online?*

A: The Northeast Consortium funded this work and they have a website with all the data from all projects they've funded. Our final report is there, but we're also developing an additional website and the interviews. Our final report excerpts some information. Some of the most interesting information is on the finer-scale details.

Q: *Why is there so little fishing on Georges Bank?*

A: Charts are specific to each peer group, and this one was trawl vessels under 65', so most aren't going to Georges Bank. We did a large set of vessels from New Bedford that shows a great deal of fishing on Georges Bank.

Curt Rice, Fisherman, Windham, Maine

I hope we all recognize fish are mobile. My fishing practices from a few years ago will not be the same this year. One of my teachers in the industry told me to throw plots away from where I had previously caught fish. I commented yesterday that we should consider our communities and social science more when we try to manage fishermen. If we have new ideas, we have to repeat them.

On the trawl survey – we found a lot of small blackback flounder. I expected to continue to find those as they grew up. Yet, we continued to find small fish. Then, we found bigger ones at a different time. In other words, we were there at the wrong time. Are we asking the right questions? Is our analysis really giving us the data we need to manage our fish?

Comments:

- I was the program manager that came out of earlier generations of that. Yesterday we were talking about managing on finer spatial scales. Madeleine made the comment that VTR data is not fine enough. So, we need to collect fisheries-dependent data on much finer scales. We're going to be limited by the data that we collect. That program is now extremely far along in development. (e.g., length distributions, anecdotal observations, scientific information) it's only limited by your ideas.
- The NMFS trawl survey has a long time record. Today we have the ability to receive data and compute patterns and to work with complex dynamics. Using fisheries dependent data, you might be able to piece together the blackback flounder story that you mentioned – not to exploit, but to manage. A decision not to fish them would be a great economic choice. I think this is a great time to be looking at fine-scale assessments based on fishery dependent data.

Ted Ames, Fisherman, Stonington, Maine

The chart that Dr. Hall-Arber left on the screen shows the western edge of where I used to fish. This is the northern crest of the Gulf of Maine. This area has stopped producing fish, and the NMFS survey did not detect it. This is because there are not smaller subdivisions in management that allow that information to be extracted. I feel this is a glaring hole.

In the mid-1980's, when fishing was good, my dealer cut me off at 50,000 lbs of fish per week, and I swore I would switch to otter trawling then because I would not have to carry an extra crewman. Our fleet was mostly 45-48' vessels and it was a very productive area and it no longer produces. The Gulf of Maine has bad management marks because part of it does not produce fish anymore. All of the spawning and nursery habitat is inside the 50 or 60-fathom line. We need a governance or management structure that allows this habitat to be protected. What Curt Rice saw during the trawl survey with small mesh net is what many of us knew before the Nordmore grate was used in the shrimp fishery because we caught everything there. We knew where juveniles and adults were located.

As fishing pressure increased and electronics improved, fish have disappeared from the entire area from Penobscot Bay east. It is not only little boats that see this problem—fishermen do as well. Fishermen who have been fishing for years in this area are a valuable resource in identifying those critical habitats so we can protect those important resources.

Q: What would you do differently? How can we rebuild the Downeast groundfish fishery by managing it separately?

A: I think we need a layered structure for management. An inshore layer to 100 fathoms, and inside that where critical habitats (nursery grounds and spawning habitat) are zoned and restricted to uses that protect habitat. Groundfish need a suit of habitats to get to the point where they've recruited to the fishery. We need to move mobile gear out and restrict them in those areas where appropriate. We also haven't addressed the eastern area of the Gulf of Maine, which was a good place to catch scallops. We have good bottom for that next to a piece of good nursery ground for codfish. This area was destroyed by our improved technology. We need different ground rules to control what we're doing. We can't look at just groundfishing—we have to look at other fisheries as well.

Q: From yesterday, looking at some of the science, the glaring hole is what's going on in Eastern Maine. We have the tools to address these questions. For cod, are they distinct? We can't get the samples to test them. I'm sure someone there could catch a few cod to test that and then we can start modeling oceanographic impacts, like dispersal and settlement. I think right now we gloss over the area because there are no fish to fish or to study there. If the fish populations started to recover, I bet there would be a lot of interest in going in to study. Newfoundland provides a good analogy, with the questions of management and forage species. I think it's wrong to assume recovery would move from inshore to offshore, which isn't really happening in Newfoundland. The assumption was that in eastern coastal Maine, the recovery would happen from offshore to inshore, and that doesn't seem to be happening. Maybe recovery has to happen right there, and we need to start looking at that.

A: Some of us have felt that what's going on is that as larvae settle in the system is where they do grow and they spawn there as well. The Penobscot River restoration happened and we started seeing fingerling cod in places where there were historic spawning grounds, so that's a recovering population that started way inside. Someone ought to be tracking it. It's still a stressed system, so it's a complex issue and there are pollution problems upstream, but something good is happening there. Penobscot East Resource Center is trying to purchase permits to develop a sentinel hook fishery in collaboration with the Department of Marine Resources and the University of Maine to do observed trips and develop a small fishery Downeast.

Comment:

- The eastern Maine coastal current is so different from the western Gulf of Maine. In western Gulf of Maine you may have a lot of retention, and in eastern Gulf of Maine you may have a lot of advection. If that's driving your system, we need to be looking upstream for where brood stock is, or the hope for recovery will be modest. We need to build the appropriate brood stock or recovery potential will be limited. It would also mean managing fundamentally different than areas that are larval sinks. One of two options is the likely case here, and if it's not one, it's probably the other. There's something driving this and we just don't have our finger on it yet.

Carl Bouchard, Fisherman, Hampton, New Hampshire

I am a day-boat dragger, and I fish from Hampton, New Hampshire, north to Boon Island and south to Massachusetts Bay. Whale Ledge – which is five by five miles – should have a fence drawn around it 5 months out of the year. It is currently closed from April to June during the rolling closures. That is the most important spawning area in the Gulf of Maine due to the oscillation that feeds down into Massachusetts Bay.

Observer data is somewhat biased. Very often fishermen behave differently when the observer is on board. The Vessel Trip report data is too vague. Throughout the day, we move around quite a bit, and VTR does not identify those fine-scale movements or our hotspots. The trawl survey sampling is so random and spaced out that it does not give accurate data in my estimation.

For example, about five years ago I was tagging for the University of New Hampshire and we were making half hour tows in April and May. On average, we were getting 500-600 lbs in a half hour tow. We made another tow and didn't get a single fish. It made me think because if the Albatross did this, it would show up as zero, yet we know there are fish there. The Massachusetts Department of Marine Fisheries inshore trawl survey that was ongoing for several years did a lot to fill the gaps. I was sorry to see it end due to lack of funding. The information that it provided was extremely valuable.

Habitat mapping is important, and a place where fishermen can be helpful to science. Out of the four of us, I'm the most fortunate fisherman in the room – we have fish in our area. I happen to live in an area where there is still good fishing.

Gary Libby, Port Clyde, Maine

There's a lot of seasonality to where we fish. Trawl survey seasons will also impact what you catch and where. Port Clyde is a unique situation where we have ten draggers left and we fish both sides of the 600 line. We all work together and belong to the same co-op. We want to maximize our profits on the fish we can catch, so we're working on direct marketing, and hopefully we'll be successful in this concept. The idea is to leave fish in the ocean to help re-populate stocks.

We discussed some of the major gaps in the discussion yesterday, but they include the lack of information on the Downeast area and the impact of dams in the rivers. The lack of eelgrass habitat and forage will make the fish move on. The 'observer effect' does happen. Some observers are great and collect good data and are friendly on the boat. Other guys sleep most of the time. Better observers would help, but fishermen also need to fill out their VTRs properly if we expect to have good science. I am also fully committed to real-time data or electronic logbooks so you get tow-to-tow data back to the scientists.

Science shows higher activity around closed areas and fishermen have been doing that for years. A lot of the fish stocks go down when copepod populations decline. We can follow fish behavior based on feed declines. If we pay attention to our estuaries, rebuild eelgrass beds and forage species and move into a progressive way of thinking, we'll rebuild fish stocks.

Comment:

- How do you get data back from arrays, protect them, and get the equipment back? Being able to work with a small group where most fishermen in the area are known and pull that data back regularly would be a good resource and reduce costs.

Q: What are your thoughts about different fishing methods and sustainability?

A: I think trawling should be limited to sand and shoal areas. We tend to stay in softer bottom. Some guys are a bit more zealous and won't be happy with it. I think much of that will be incorporated into the sector rules we're developing. We might want to experiment with hooks, or a gillnet fishery that would catch less juveniles. I will consider doing whatever it takes to stay on the water. If trawling is damaging too many things, then I can switch. The Downeast areas and scallop fisheries are in poor health but we're looking at area management for the scallop fishery and we may learn more after that plan goes into effect.

Q: We should remember the community of fishermen and keep in mind what's happening to co-ops and markets. Is Port Clyde willing to be a leader and help set up sectors or co-ops?

A: Yes, we're doing a Community-Supported Fishery (CSF) program through our co-op that's all about community. The Portsmouth fishermen should have the opportunity to supply their community with fish the way we do. We need to support communities and community fishermen to keep them in business to catch less fish and make more money per fish.

Dr. Jim Wilson concluded the panel by noting that, until the end of the day, most of the discussion had been species-specific discussion and observations from the scientific community. At the end of the day, Gary Libby raised the ecosystem question. Fishermen seem to have more to say about the system than the scientists do. Why is it that science seems to have to become species-specific whenever limits are posed? Every scientist in this room is ultimately interested in the system, so how do we link the fishermen's observations and fine scale information about the system and integrate it into our science about the oceans?

Reactions and Discussion

This is too big a question to answer, but not to ask. Typically you have science understanding patterns of distribution and abundance. Asking that about just one species is hugely complex. Once you do it for one species, you have to do it for others. Presumably we could get to the point where we asked, in what demographically significant ways are they interacting? We are just beginning to go down this path, and the science is not yet mature enough to address ecosystem-scale questions. I do not think the big models are going to be instructive when we look at things like Dr. Hall-Arber's fishing maps. We need to think about how to resolve small manageable areas before we try to scale up to the entire Gulf of Maine.

If the question is too big to answer with science, should we be trying to answer it with something else? Perhaps we should look at social science and the community side of things, like aligning incentives of fishermen to do right thing with what we do know about how the system works and putting fishermen's knowledge to work.

I work with the Cobscook Bay Resource Center. The Cobscook Bay Fishermen's Association is broader than its membership and they view Cobscook Bay as an ecosystem. They now identify with Cobscook Bay—it is the ecological address that makes sense to them, when previously the area was referred to as Quoddy Region. Now they see everything as interconnected in Cobscook and they understand current/drift studies and it makes more sense to them because they're involved in the work. Those 20 people have demonstrated the potential of identifying with a place and an ecosystem not just for one fishery but across all of them. When you can get fishermen together talking about these issues, everyone will be better off in the long term, particularly if the local knowledge can be applied to a bigger system.

Every tow we make, we know we're scraping a biological community. We need to know how and why species are interacting. This is something that needs to be done over the long term.

The loss of large fish is the big loss. Why aren't they coming back as adults, where are they going? We need science and fisheries to answer those questions.

Communication between science and fishermen is critical. We heard many viewpoints and approaches to questions related to cod. The fishermen are not afraid to ask about the whole system. Scientists find it harder to be sure about the answers because of the levels of complexity, so they want to study the details carefully. Communication between the two will give us the answers we want.

We did a project in Passamaquoddy Bay looking at historic cod fishing areas, and we didn't find any cod there but we found lots of sculpin. It is information I take to demersal ecologists, but finding the right person can be challenging. You need a diverse group of scientists in the room to answer these questions but sometimes there can be too many.

Fishermen have unique knowledge and connect grounds because they have information that's not only historical but also from his knowledge of the bottom and his experience on the water.

These are great examples of the need for both fishermen's knowledge and technology. We've identified that this ecosystem is complex, chaotic and science is uncertain. Even with a lot more knowledge, the science is probably still going to be uncertain. I think we can use the advantages of local knowledge to develop hypotheses, but it wouldn't be valuable to simply abandon the science [and move towards a community scale approach entirely based on human behaviors].

Reports From Breakout Groups

Breakout groups of 12-15 participants convened for discussion addressing the following questions:

- What additional research is needed to make informed decisions about appropriate scales for groundfish management?
- What long-term monitoring data do we currently have, and what additional parameters might be required if we were to move to finer scale management?
- What changes in assumptions or assessments are necessary to manage at a finer scale and what are the challenges inherent to making those changes?
- Do we know enough from research and monitoring to pursue a management shift towards a finer or different scale?

Laura Taylor Singer summarized the breakout group work in a brief wrap up at the end of the workshop's second day.

Several themes emerged from the discussions to address what additional research might be needed in order to consider alternate ecological scales. The first theme focused on the need for rapid assessment, whether through fishery dependent data or standardized environmental data monitoring. Real-time catch data or telemetric collection could be utilized for this purpose. This type of rapid assessment could also be used to identify bycatch hotspots, redirect fishing effort and inform research priorities. Another theme emphasized the importance of adding value to the question of appropriate ecological scale through data synthesis. This integration could be done using place-based linkages, across disciplines, using study fleets in discrete fishing communities and could include social sciences as well as physical sciences. Many groups noted the need to improve understanding of predator/prey relationships and food web linkages. How do groundfish, particularly larvae and juveniles, utilize habitat? What role do fishermen play as predators in the ecosystem? Additional socio-economic information is also a critical need.

The second question focused on new applications of existing long-term monitoring data and additional needs. Breakout groups identified the need to address the challenges of even distribution assumptions by integrating habitat and substrate maps into stock assessments to link habitat with life history stages, which might suggest that a different assessment methodology is appropriate. New survey techniques should be utilized to sample areas underrepresented due to limitations of trawl survey to sample certain habitats. The observer program's data collection protocols might also be modified to better serve the industry, potentially improving the relationship between observers and fishermen.

There are a number of steps that need to be taken in order to determine whether an alternative scale is appropriate for groundfish management. First, we must define what we mean by the concept of "fine scale." We need to obtain more fishery dependent data and make better use of that data, through Study Fleet work or otherwise. We must also find creative ways to expand our use of the current assessment data, as there is value in the time series and size of the dataset. This also touches on the question of funding—we must proceed on the assumption that additional funding is unlikely, or that to increase funding to assess at a finer scale we would have to sacrifice funding for other work. We must take an adaptive approach to the process of determining appropriate scale. Finally, we should continue this discussion in another workshop to discuss management and governance questions as they relate to scale, and involve the New England Fishery Management Council and NMFS staff in those discussions, recognizing that a finer scale of management might cause greater complexity in management.

As to the question of whether we know enough to move to a finer scale of assessment or management, the emphasis was placed again on the importance of using adaptive management strategies. A great deal is known, and we could begin to manage at alternate, or finer, scales and re-assess as necessary. We could test alternate scale management projects through pilot projects in Penobscot Bay or with the Port Clyde fleet.

Conclusion

The day's discussion led to at least one strong message: that management should be tailored to the appropriate ecological scale, but this might require management of multiple scales, not just a finer scale. Our current management system misses a medium and finer scale, but we also need to maintain a picture of the whole system. We should not move to a system that manages many smaller boxes at a smaller scale, but rather should incorporate the approaches of alternate scale to promote ecological and financial sustainability. Any shifts in management will require stewardship effective management and enforcement mechanisms, as well as an understanding of the socio-economic impacts associated with those shifts.

APPENDIX A

Stock Structure of New England Groundfish – connectivity and heterogeneity at multiple scales, Steve Cadrin

Dave Martins, Jon Loehrke, Lisa Kerr, Greg DeCelles, Dan Goethel and Crista Bank. NOAA/UMass Cooperative Marine Education & Research Program School for Marine Science and Technology, 200 Mill Road, Fairhaven, MA

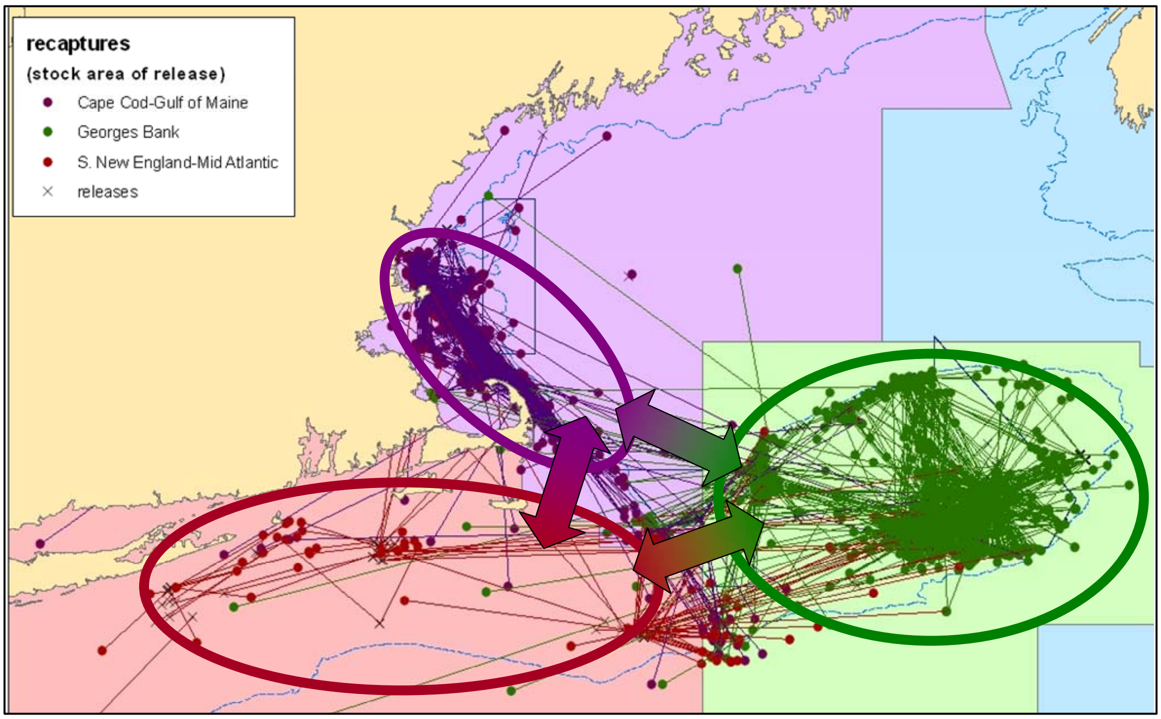
Many ecological processes occur at fine spatial scales, such as feeding, spawning, larval dynamics or habitat-mediated events. However, many fundamental concepts of stock assessment and fishery management pertain to larger-scale processes. For example, 'overfishing' applies to an entire management unit or stock, but the concept becomes less meaningful as the management unit is subdivided into smaller and smaller units. At the individual level (the extreme subunit), 'overfishing' is meaningless, because every fish that is harvested is overfished. A challenge for effective fishery management is determining the spatial scale at which to monitor and model population dynamics.

The appropriate spatial scale for defining self-sustaining stocks depends on the spatial extent at which biological production operates. Stocks are delineated such that production is primarily determined by factors within the area rather than influences from outside the area. For example, recruitment should be produced by spawners within the stock, rather than by spawners from nearby stocks. In practice, intraspecific marine populations are seldom completely isolated from other populations, and stock identification involves a balance between considering heterogeneity within stocks and connectivity among stocks.

A conceptual view of population structure for each species is important for determining management units and appropriate spatial scales. General forms of population structure include 1) single, large populations that have homogeneous vital rates and are panmictic (i.e., all individuals can randomly mate); 2) metapopulations that include reproductively connected subpopulations; and 3) reproductively isolated subpopulations that are either allopatric (i.e., geographically separated) or sympatric (i.e., spatially overlapping). New England groundfish species represent all three of these theoretical population structures with some important complexities that deviate from general theories.

Most groundfish species are managed as a single U.S. or transboundary stock (witch flounder, American plaice, white hake, pollock, Acadian redfish, ocean pout, and Atlantic halibut). For some groundfish species, management unit definitions are based on apparent homogeneity of vital rates (American plaice and white hake), others are based on tagging studies that show extensive movements within or beyond the region (white hake, pollock, and halibut), and the rest are essentially data-poor defaults (e.g., ocean pout). Despite the apparent genetic homogeneity of some groundfish species in the New England region, they often form cohesive behavioral groups, called contingents that have important consequences on population productivity, stability and resilience. For example, Pollock form local, inshore spawning groups, but movement is widespread across the Gulf of Maine.

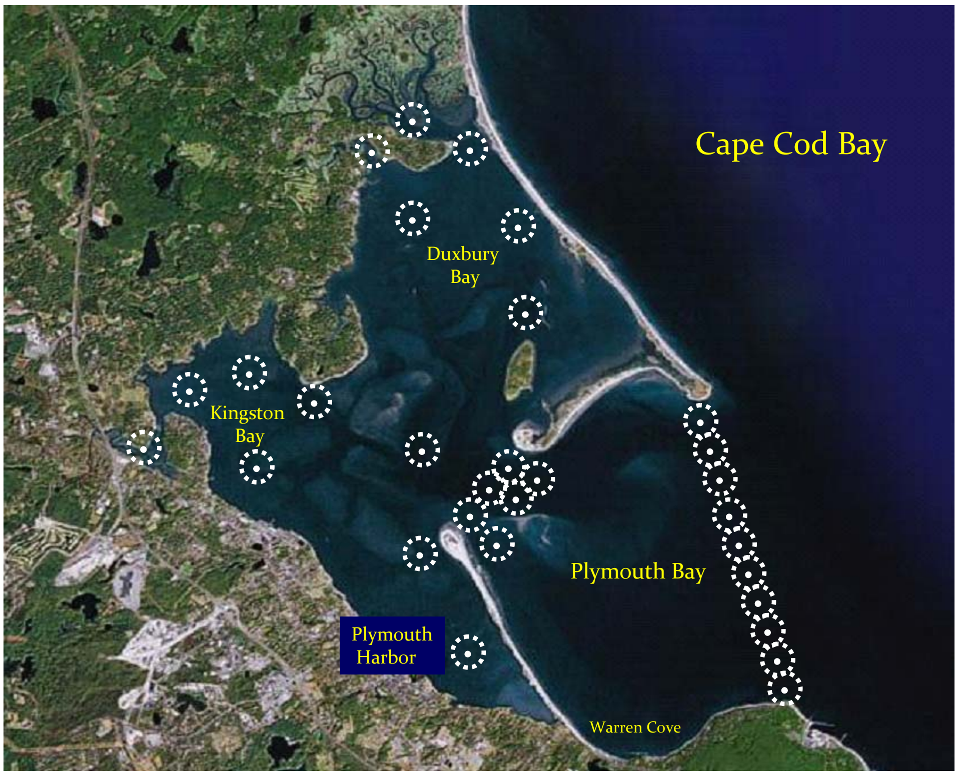
Yellowtail flounder off New England appear to form a metapopulation, because genetic differences have not been found among subpopulations, and there is some connectivity among subpopulations in the form of larval drift and adult movements. However, subpopulations are isolated enough to maintain different vital rates (e.g., slower growth and maturity in the Gulf of Maine than on Georges Bank) or different demographic patterns (e.g., dominant year-classes). Metapopulation models informed by tagging data suggest that production of yellowtail in the Cape Cod-Gulf of Maine yellowtail stock may be particularly sensitive to even small rates of movement from the larger subpopulations on Georges Bank and off southern New England.



The yellowtail flounder resource viewed as a metapopulation, with stocks as connected subpopulations (ellipses) and observed movements from tagging data.

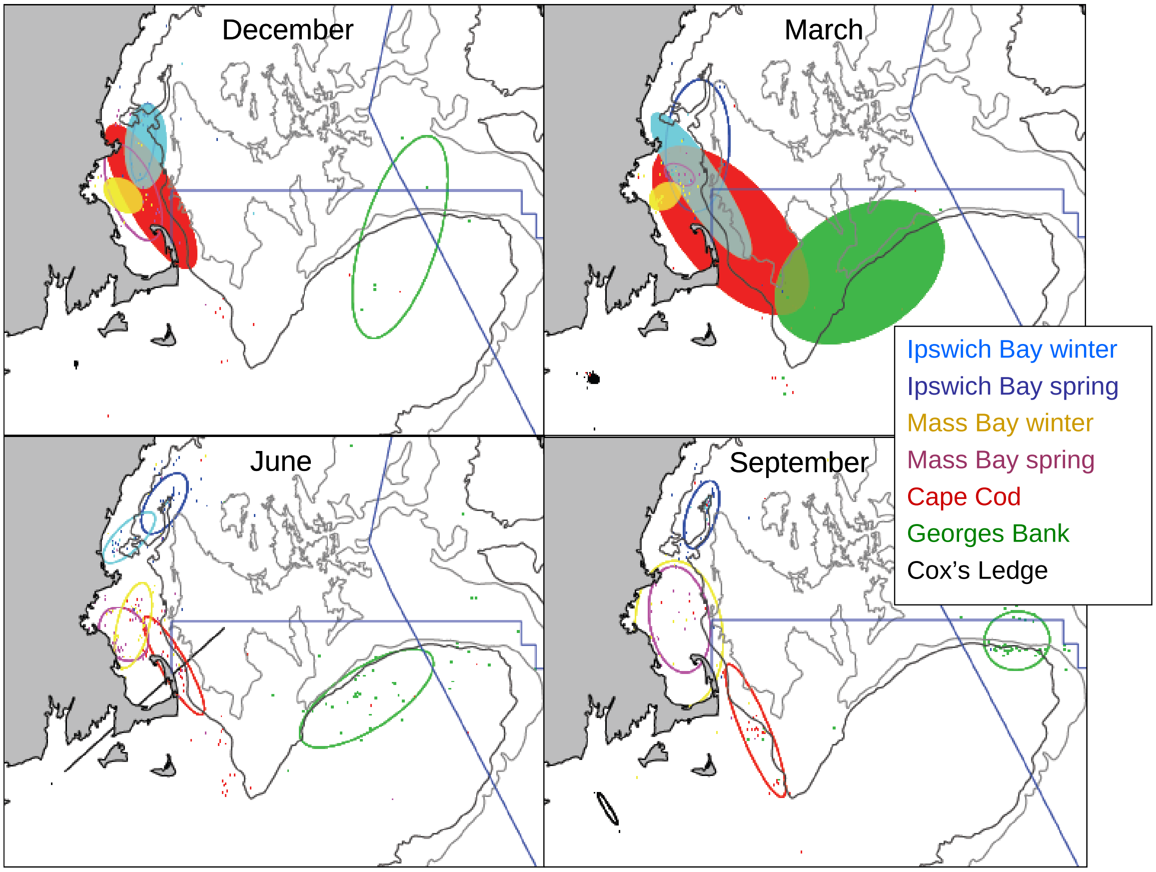
Allopatric patterns of population structure are not likely within the Gulf of Maine area, because there are no geographic barriers that completely isolate subpopulations, and there is some mixing of planktonic or post-settlement stages within the region. Allopatric structure of marine populations is usually a more broad-scale pattern, such as separation of northwest Atlantic cod from northeast Atlantic cod.

Winter flounder form sympatric subpopulations, with genetically distinct estuarine, coastal or offshore spawning groups that overlap after spawning. The fishery targets a mixed-stock resource in coastal waters, which is managed as two coastal stock complexes (in the Gulf of Maine and off southern New England-Mid Atlantic) and a single offshore resource on Georges Bank. Production among subpopulations varies, with those off the Maine coast being severely depleted, while those in western Gulf of Maine being more productive. Another more recent trend observed in the Gulf of Maine is a general transition from estuarine spawning habitats to coastal spawning habitats. Acoustic telemetry offers a valuable tool for studying patterns in habitat use, residence time and spawning areas of winter flounder.

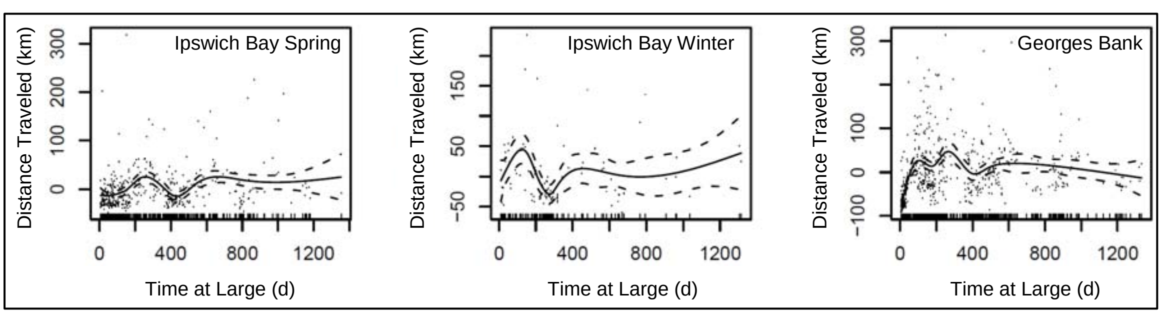


Acoustic array deployed in the Plymouth Bay system to monitor habitat use and spawning dynamics of developing winter flounder tagged with transmitters in Warren Cove and Duxbury Bay.

Throughout its geographic range, Atlantic cod present a challenge to determining the scale at which the fishery should be managed. The population structure of cod may be best described as dynamic sympatry, because genetically distinct spawning groups overlap with seasonally shifting distributions, and different spawning groups have different dispersal patterns. Tagging studies suggest that the mechanism of reproductive isolation is natal homing to distinct spawning grounds (e.g., Ipswich Bay vs. Massachusetts Bay) or seasons (e.g., Ipswich Bay winter vs. Ipswich Bay spring). The failure of productive spawning groups in the western Gulf of Maine to repopulate traditional cod habitat off eastern Maine suggests that spawning groups are not reproductively connected and are adapted to distinct migration circuits. Although some resident spawning groups of cod may be effectively assessed and managed as local stocks, it would be misleading to consider other spawning groups in the same area as a local resource.



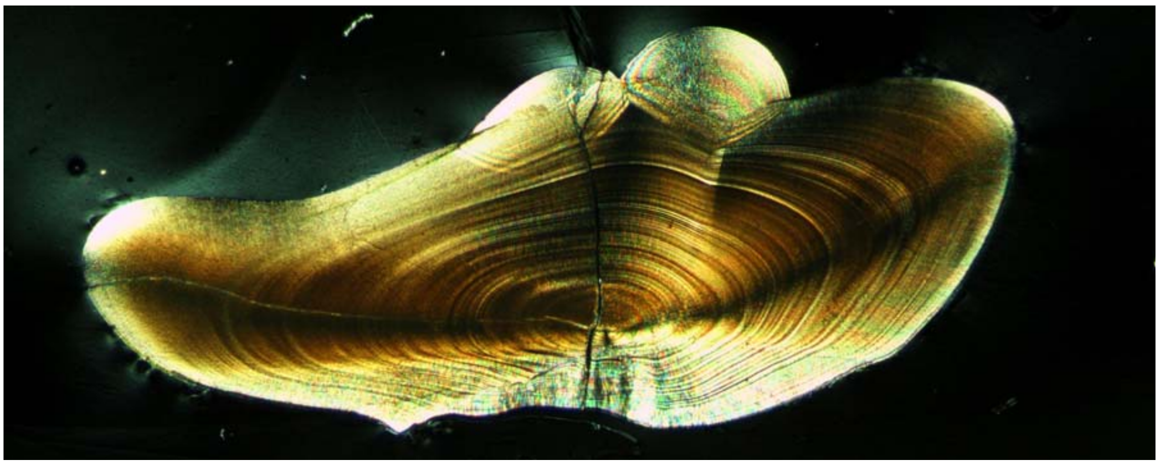
Seasonal distribution of recaptured cod that were tagged on spawning grounds during spawning seasons. Ellipses contain 50% of the recaptures by spawning group, solid ellipses are during the spawning season for each spawning group, and open ellipses are not.



Dispersal patterns of tagged Atlantic cod from three spawning groups off New England showing varying degrees of natal homing. Cyclic splines (solid curved lines) and their confidence limits (dashed lines) indicate that

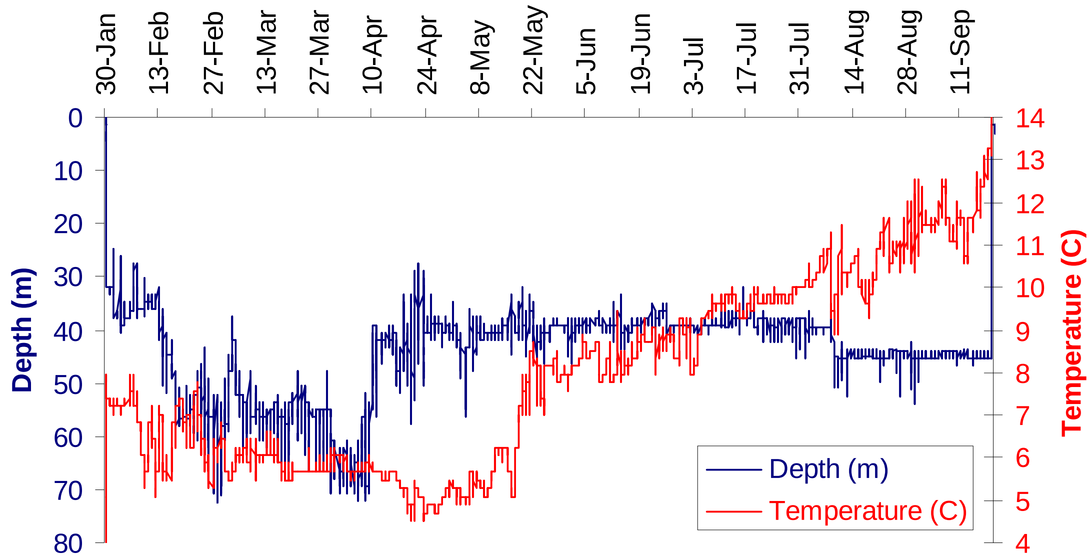
homing is strong in Ipswich Bay, because cod are recaptured near their release location after a year at large.

Other fishery resources that exhibit dynamic sympatry are effectively managed at multiple scales using stock composition analysis. However, further work is needed to identify 'natural tags' (e.g., genetic characters, otolith microstructure or otolith chemistry) to apply stock composition analysis of cod off New England. For example, preliminary research on otolith microstructure of age-0 cod suggests that recruits can be classified to seasonal spawning groups by circuli patterns, and otolith chemistry may identify spawning groups based on geographic and seasonal differences in the chemical composition of otolith cores.



Otolith of an age-0 cod sampled from the Massachusetts trawl survey showing daily growth circuli.

Understanding the environmental cues that initiate dispersive and homing behavior can help to develop an accurate view of cod's dynamic sympatry. One tool that can be applied to explore behavioral cues is electronic tagging. Data from archival tags can be used to identify seasonal depth and temperature habitats, geolocate fish during tag deployment, and reveal environmental signals associated with movements.



Depth and temperature recorded from a DST deployed on cod spawning on Cox Ledge in January 2007. The fish moved to deeper water in the spring, then was recaptured back on Cox Ledge in September.

Although many aspects of groundfish ecology are manifest at small spatial scales, and small-scale management could benefit from local ecological knowledge of the resource, many critical aspects of population dynamics occur at more regional scales. The scientific cost of defining management units too finely is that emigration of fish from a local unit will be interpreted as mortality, and immigration will be interpreted as recruitment. The cost of defining stocks too broadly is the failure to recognize and address important patterns of heterogeneity within the stock. Therefore, the science of stock identification involves determination of practical boundaries that delineate major patterns of heterogeneity while minimizing connectivity among units.

Extended Abstract – Acoustic Arrays and Cod Stock Structure, Martin Castonguay

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Tracking movements of animals at sea in deep water for long periods has long posed problems. Conventional tagging is sometimes insufficient but can be supplemented by acoustic array technology, which involves the acoustic tagging of fish in the cavity along with the deployment of acoustic arrays in strategic locations to monitor movements of tagged fish. Low cost makes it feasible to acoustically tag large numbers of individuals to make inferences at a population scale. We present three studies that used such technology to shed light on cod stock mixing and population structure issues to assist fisheries management. The first study involved stock mixing between southern Gulf of St. Lawrence (4T) and Sydney Bight cod (4Vn). We found that cod migrated all over the 160 km line of array and that it was unlikely that the winter trawl fishery would target a high proportion of the depleted Sydney Bight stock.

The second study involved winter mixing between cod from the northern Gulf of St. Lawrence (Divisions 3Pn4RS) and cod off southern Newfoundland (Division 3Ps), which may slow down cod recovery in the Gulf. The purpose of this study was to estimate mixing rate of northern Gulf cod into southern Newfoundland. We deployed a total of 80 receivers near bottom every mile that covered the entire distance along management lines separating Divisions 3Pn and 3Ps, and 4R and 3Pn. Two additional shorter receiver lines were also deployed on Burgeo and St. Pierre Banks. Based on two independent measures of receiver detection efficiency (0.76 and 0.83), we estimated the percentage of northern Gulf cod crossing into 3Ps in the fall to be 61%. The main month that Gulf cod entered 3Ps was December while the main month of return to the Gulf was April. This study provides the first firm evidence that the majority of northern Gulf cod mixes with 3Ps cod in winter and that northern Gulf cod are present in 3Ps in April when the research vessel survey is carried out there, which may bias survey results. Current closures in winter in 3Ps to account for mixing appear quite adequate in protecting 3Pn4RS cod.

The last study involved acoustic tagging of northern cod to shed new light on stock substructure. Offshore tagging and telemetry in 2008 indicated that a substantial portion of cod from the offshore aggregation migrated to the inshore of 3KL during summer, rendering them vulnerable to inshore fisheries. Exploitation of offshore cod in the inshore was estimated at 6%. Management of inshore and offshore as separate components is clearly no longer consistent with new information on cod migration from tagging and telemetry.

Extended Abstract - Genetic Insights into the Stock Structure of Atlantic Cod in US Waters, Adrienne Kovach

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Marine species have long been viewed as open, panmictic populations with high connectivity, owing to their vagile, pelagic larval stages and the high migratory potential of adults. This classical view of marine species was supported by tagging studies, which demonstrated long distance migrations, and by early genetic studies that revealed high levels of gene flow, as expected for a marine environment considered to be free of dispersal barriers.

Recently, there has been a paradigm shift in the view of the population structure of marine species, articulated by a review by Hauser & Carvalho (2008). Overwhelming evidence now points toward the existence of population structure on fine geographic and temporal scales. A growing body of literature emphasizes the importance of process, such as sedentary life history strategies, spawning site fidelity, natal homing, adaptations to local environmental conditions, and ocean currents and bathymetric features promoting egg and larval retention; the effect of these processes is to limit dispersal and promote self-replenishment of local populations, leading to subdivision and potentially reproductive isolation. Additionally, evidence of multiple life history strategies within a population, such as temporally divergent spawning behaviors or inshore *vs.* offshore migration patterns, have also been linked to fine-scale population structuring in cod, herring and other marine species.

The implications of the different paradigms are significant for management. The current management models are typically based on the “old dogma” of panmictic populations, and do not consider fine-scale population structure. Stocks encompass large geographic regions with multiple oceanographic features and may be comprised of individuals with potentially different life history histories. As such, their boundaries may not have a biological basis. This may be true for cod in U.S. waters, which are currently managed according to a two stock model, consisting of (1) a Gulf of Maine stock and (2) a stock comprised of Georges Bank and areas southward, from southern New England to the mid-Atlantic coast. Evidence inconsistent with the current management model includes movement data from recent tagging studies (Tallack and Whitford 2008) and genetic data (Lage et al. 2004, Wirgin et al. 2007).

In our previous work (Wirgin et al. 2007), we found heterogeneity within the Gulf of Maine, stemming from temporally divergent inshore spawning populations. A spring spawning population in Ipswich Bay was genetically distinct from winter-spawning cod from all other sites within the Gulf of Maine (including the same bay), Georges Bank and sites in southern New England. We also found that cod spawning on the northeast peak of Georges Bank are differentiated from populations south of Cape Cod, consistent with an earlier finding by Lage et al. (2004). Whether these differences were stable over time, or merely reflected variation among cohorts or plasticity in spawning behaviors, remained an open question.

In the current study, we expand on our previous efforts with increased and replicated sampling over time, in order to develop a model of population genetic structure of cod in US waters. *Our objectives were to 1) identify and sample all current spawning aggregates, 2) characterize the fine-scale population structure of spatially and temporally separated spawning aggregates, 3) investigate the temporal stability of the genetic structure, using replicate samples collected over a 2-5 year period, and 4) determine whether young of the year fish sampled on juvenile nurseries could be assigned definitively to their populations of origin.*

This research was truly collaborative in nature, not only with respect to contributions to the genetic analyses from both UNH and NYU, but also with respect to the sample collection. The latter involved numerous commercial fisherman, supported by the collaborative research program of the Northeast Consortium, recreational fisherman, and fisheries biologists from the Massachusetts Division of Marine Fisheries, Canadian Department of Fisheries and Oceans, and also a partnership with the University of Massachusetts-Dartmouth School for Marine Science and Technology.

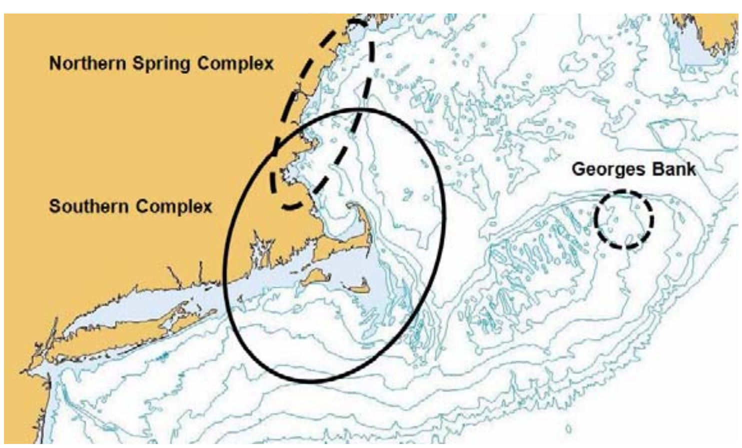
During December 2005 – July 2008, 1488 adult cod were captured via otter trawl, gill net or hook and line; a fin clip was taken for genetic analysis. We targeted spawning fish from the following sites: northeast peak of Georges Bank, the inshore Gulf of Maine in Ipswich Bay, Massachusetts Bay, and Bigelow Bight, ME, the offshore Gulf of Maine at Jeffrey's Ledge and Stellwagen Bank, and south of Cape Cod from Nantucket Shoals, and Cox Ledge. At Ipswich Bay, Massachusetts Bay and Coxes Ledge, distinct spawning aggregates were identified and sampled in both the spring and winter. Additionally, adult fish not in spawning condition were sampled from Ipswich Bay, Platts Bank (offshore ME) and New York Bight. Six of the spawning aggregates were sampled in 2 subsequent years, enabling a test for stability in the structure.

Genetic analysis of the fin clip-extracted DNA was performed using a panel of 10 microsatellite markers (*Gmo*02, *Gmo*132, Brooker et al. 1994; *Gmo*19, *Gmo*35, *Gmo*36, *Gmo*37, Miller et al. 2000; P*Gmo*32, P*Gmo*34, P*Gmo*38, and P*Gmo*58, Jakobsdóttir et al. 2006), and 6 SNPs (Pantophysin I (*Pan* I), Pogson et al. 2001, *AHR6*, *ARNT8,* Wirgin et al. 2007*, and ARNT1*, *CYP5*, and *K ras,* characterized in this study). Several statistical population genetic methods were employed to analyze the genotypic data, including F-statistics (FST, a measure of genetic variation among populations), allelic differentiation exact tests, and molecular analysis of variance (AMOVA), to test for hierarchical structure and temporal variability.

Results of pair-wise population F_{ST} comparisons and AMOVA indicated there was no significant variation between the yearly collections from the same sample locations and that variation among sites was significantly greater than annual variation within sites; therefore, these samples were pooled for further analysis. These findings are evidence for stability in the genetic structure over time.

When the pooled data from all spawning aggregates were compared by pair-wise F_{ST} analysis, 16 of 45 population comparisons were significant. The primary source of differentiation occurred between the spring spawning coastal aggregates of the inshore Gulf of Maine (Ipswich Bay, Massachusetts Bay and Bigelow Bight) and sites in the offshore Gulf of Maine, winter spawning inshore Gulf of Maine and southern New England sites (Nantucket and Cox Ledge). Additionally, Georges Bank was strongly differentiated from the southern sites. The significant F_{ST} values ($P<0.001$, following Bonferroni adjustment) ranged from 0.0071 – 0.0156, consistent with findings from other studies reporting weak, but significant differentiation for cod in European and Canadian waters (Beacham et al. 2002, Westgard & Fevolden 20007) over similar small geographic scales. Evaluation with the less conservative $p < 0.01$ and the exact tests yielded 13 additional, significant comparisons for F_{ST} values in the range of 0.0017 – 0.0076, consistent with the level of fine-scale structuring documented among adjacent fjords in Norway (Jorde et al. 2007). Visualization of results with a principle coordinate analysis (PCA) demonstrated that the spring spawning inshore GOM sites clustered separately from the winter spawning inshore GOM, offshore GOM and southern sites, with Georges Bank positioned somewhat intermediately. Comparison with our data from 2003-2005 of Wirgin et al. (2007) showed consistency in the genetic composition of sites sampled in both studies, further supporting the temporal stability of the population genetic structure we identified.

The majority of the genetic variation in this study can be explained by three major groupings: a <u>northern spring coastal complex</u> that consists of spring spawners in coastal GOM, a <u>southern complex</u> that consists of winter spawners in coastal GOM and winter and spring spawners in the offshore GOM and southern New England, and the <u>northeastern Georges Bank</u> spawners (see figure). The Georges Bank population was strongly differentiated from the southern sites, and only weakly so from the inshore GOM and similar to the offshore GOM. In addition to the significant variation among the complexes, we also found significant variation within complexes ($p<0.0001$, using AMOVA, molecular analysis of variance), indicating the presence of finer scale population differentiation.



We consider several mechanisms as potentially important in generating the fine-scale genetic population structure that we observed. 1) Temporal differences in spawning may have a genetic component, rather than being plastic (Bekkevold et al. 2007); this is further supported by studies of captive populations that continue to spawn at divergent times, despite similar environmental conditions (Ottera et al. 2006). 2) The genetically divergent populations may exhibit alternate resident and migrant strategies (Robichaud & Rose 2004). Howell et al. (2008) recently showed that most spring-spawning cod in Ipswich Bay are sedentary residents. The winter spawning and offshore populations may be more migratory. 3) Spawning site fidelity may be common, but some individuals may exhibit natal homing, which facilitates reproductive isolation, while others may behave like “adopted migrants” (McQuinn 1997), whereby they follow the migratory behaviors of nearby populations to which they disperse and recruit as juveniles. 4) Environmental forces that affect the dispersal of early life stages or the migrations of adults may differ among seasons or for inshore *vs*. offshore. For example, larval dispersion models have shown that wind patterns in the GOM in the spring and summer favor local retention, while those in the winter may force larvae to drift with the currents offshore (Jim Churchill, Woods Hole Oceanographic Institute, personal communication). 5) Lastly, the genetic structure revealed by the markers today reflects a historical signal in the data set, such as postglacial population expansion; the low genetic differentiation in general may reflect a relatively recent history of Atlantic cod populations (Pampoulie et al. 2008).

The majority of the genetic differentiation in this study can be attributed to 2 highly informative markers, Pan I and Gmo132, which had much higher per locus FST values than the other markers (0.038 - 0.109 and 0.028 – 0.043 for Pan I and Gmo132, respectively, in comparison to 0.0012 for the mean of the other loci combined). These two markers have been previously shown to be under selection (Nielsen et al. 2006, Pogson 2001), in contrast to most genetic markers used in population studies, which are presumed neutral. Results of FST outlier selection tests confirmed that these loci were under selection in our study as well. The differentiation of the major spawning groups could be explained by differing allele frequencies of the Pan I A allele, which was higher in the northern spring complex than the southern complex or Georges Bank, and the Gmo132-117 and 135 alleles, which differed in the southern complex relative to the northern spring complex and Georges Bank.

It is suspected that Gmo132 is linked to a gene with unknown function (“hitch-hiking selection”; Nielsen 2006). Pan I is located in a gene that codes for a protein found in the membranes of microvesicles (Pogson 2001), but its relevant function in fish is unknown. Pan I A & B allele frequencies follow different patterns across the range of cod. Variation at Pan I has been correlated with numerous factors, including temperature, salinity, depth, growth and migratory behaviors. The covariates, however, differ among geographic locations; for example, while the Pan I A allele has been linked to warm waters in Norway (Westgard & Fevolden 2007), in Iceland it’s the Pan B allele that dominates under those conditions (Pampoulie et al. 06). In our study, no consistent pattern was evident for temperature, salinity or depth in relation to the observed genetic variation, and the variation in these potential factors was small among our populations. A correlation of the Pan I B allele with offshore migrations or spawning has been found in populations in Norway, Iceland and Canada. This relationship is consistent for our study, in that populations with the highest Pan I B allele are found in the southern complex and Georges Bank, the populations that spawn offshore or are most likely to undertake offshore migrations. However, the differences in allele frequencies were small, with the frequency of the Pan I B allele occurring at 0.85-0.90 in the northern complex and near fixation in the southern complex and Georges Bank. A correlation with growth cannot be ruled out, as size differences have been documented for the GOM vs. other populations (Tallack & Whitlock 2008), however, to our knowledge growth data do not exist for the seasonally divergent spawning groups.

In conclusion, we found strong evidence for population genetic structure that is not consistent with the 2-stock management model. Cod in US waters are broadly structured into 3 groups: 1) a northern spring spawning coastal complex in the GOM, 2) a southern complex consisting of winter-spawning inshore GOM, offshore GOM and sites south of Cape Cod, and 3) a Georges Bank population. These groups are temporally stable and the magnitude of genetic differentiation, while not large, is sufficient to assign juveniles to their population of origin via mixture modeling. Genetically distinct groups overlap spatially in the inshore GOM, but are separated by temporal divergence in spawning behavior. We also found evidence of finer-scale structuring within the southern complex. Our results also support earlier findings that the Great South Channel may be influential in separating populations on the northeast Georges Bank from those south of Cape Cod. We suggest that several mechanisms are operating simultaneously to produce the population structure. Our finding that the majority of the differentiation is attributed to two non-neutral loci, points to the importance of local ecological adaptations. The particular selective forces shaping the adaptive divergence, however, are yet unknown and warrant further study.

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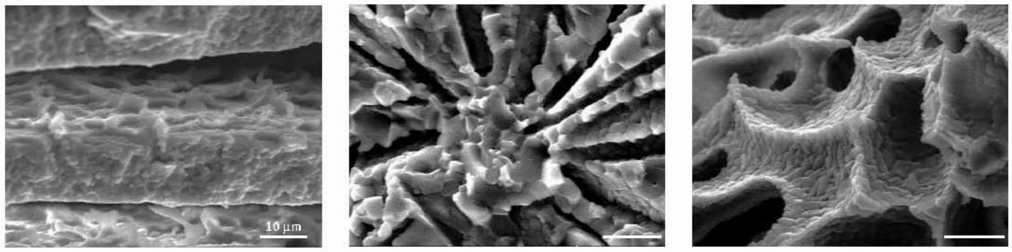

Ice templates. (Left) Nacre-like layers after removal of ice dendrites from solidification of alumina suspension in water. [Adapted from (*12*)] **(Center)** Starburst voids after removal of naphthalene dendrites from solidification of alumina suspension in camphor-naphthalene, which do not provide a template for tough composites. **(Right)** Branching voids after removal of camphor dendrites from solidification of alumina suspension in camphor-naphthalene.

fibrous laminates (*11*) that were in fact much tougher ceramics. However, these were tedious to manufacture and limited in the suite of materials. On page 515 of this issue, Deville *et al.* report a better route, using simple freezing (*12*).

Deville *et al.* have shown how to replicate the nacre structure of shells using controlled freezing of mixtures of water and ceramic powder. The composites made by this route have remarkably improved mechanical properties. The researchers achieve this by combining conventional manufacturing approaches that are already part of the engineering toolkit. These are as follows: (i) fine powder processing, the mainstay of the ceramic industry; (ii) controlled solidification, the core capability for metal casting and the frozen-food industry; and (iii) freeze-drying, a routine technique in the chemical, food, and coffee industries. Their nacre-like composites start with a lamellar template assembled by ice crystals. Water freezes as lamellar dendrites (*13*), and the ice dendrites push the ceramic particles into the interdendritic regions, making layers on the same scale as the ice. After the ice is removed by freeze-drying, the ceramic keeps the shape of the interdendritic layers, forming a template for subsequent injection of tough metal or polymer. The choice of water is clever, as the lamellar ice dendrites make an excellent template for nacre (see the figure, left panel). Other media are not useful templates, forming starburst dendrites as with naphthalene (see the figure, middle panel) or branched dendrites as with camphor (see the figure, right panel).

The technology for controlling dendrites is commonly used in applications ranging from the improvement of exotic jet-engine alloys to creating a tastier texture in frozen desserts. With the scale and arrangement of dendrites determined by well-known physics, and pattern formation well understood, there are many opportunities to build on the ideas of templating composites with ice. The methods of Deville *et al.* promise a flexible strategy for combining what people can do in factories with design concepts inspired by biology.

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ECOLOGY

Staying Connected in a Turbulent World

The swimming behavior of fish larvae limits their dispersal among coral reef populations more than previously thought. This stands to affect the design of protected marine ecosystems.

Robert S. Steneck

Globally, coral reefs are endangered ecosystems that continually frustrate marine resource managers and policymakers charged with their protection and restoration. Sadly, we know much more about the frequency, intensity, and scale of coral reef degradation (*1*) than we do about the processes that drive their recovery (*2*). This is most noticeable among Caribbean coral reefs that have particularly low resilience in both resisting phase shifts to degraded states (*3*) and, once degraded, in returning to their previous state (*4*). A study by Cowen *et al.* on page 522 in this issue (*5*) offers new insights into the spatial scale and rate of larval supply necessary to sustain Caribbean reef fish populations. Cowen *et al.* improved on past population "connectivity" models by developing a coupled biological-physical approach that integrates factors such as the duration of development and swimming behavior of larvae, together with a well-validated model of ocean currents. They determined that connectivity, or the nexuses among disjunct populations of reef fish, is more local and regionally more variable than previously thought. These simple but profound results influence the scale at which coral reefs should be managed and identify regions that will likely be more resilient or more vulnerable to the effects of fishing. The results scale up to regional (ocean-basin scale) considerations of biogeography, genetic isolation, and invasions of nonnative species that apply to fish and potentially to other reef-dwelling organisms, including corals.

The model developed by Cowen *et al.* improves upon the work of Roberts (*6*), a highly influential paper on connectivity and the management of Caribbean coral reefs, that considered primarily passive transport of fish larvae via ocean currents in order to estimate

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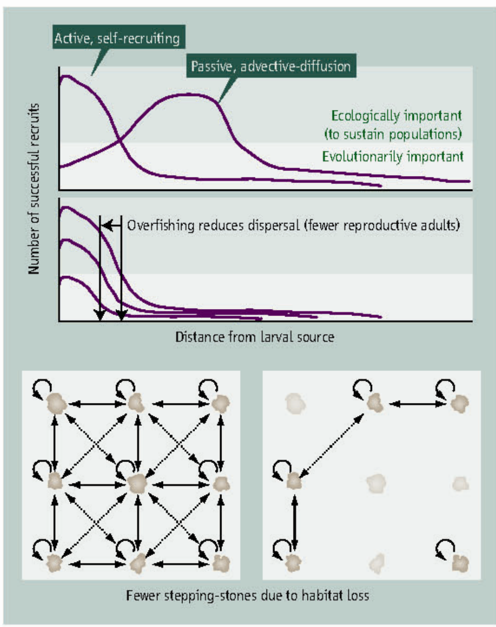
the maximum range of larval connectivity among coral reefs. Roberts viewed many populations of marine organisms as being relatively open with substantial subsidies from distant upstream populations. In contrast, Cowen *et al.* have determined that larval transport via passive-diffusion cannot sustain reef fish at current levels unless there is substantial self-recruitment that results from the behavior of fish larvae themselves. The more realistic connectivity model of Cowen *et al.* provides the first robust estimates of the distance larvae will probably travel to successfully recruit to a specific reef [called the dispersal kernel (see the figure)]. Because a large portion of the larvae are recruiting at or near the reef where their eggs were hatched (that is, "self-recruiting" to the reef of larval origin) and because larval mortality will diminish the number of surviving larvae with time and distance from the larval source (*7*), the dispersal kernel will usually be greatest near the region where eggs were hatched and decline with distance. Conversely, passive advective-diffusion models will result in larvae being transported, and thus their kernel dispersed, some distance away from their places of origin. The Cowen *et al.* model operates at several spatial scales and identifies distinct subregions within the Caribbean that have different levels of larval subsidies and self-recruitment. The finding that larval subsidies are very limited in some regions suggests that marine resource managers must directly manage their reefs on a local scale and not depend on substantial larval subsidies from distant upstream sources.

Another advantage of the Cowen *et al.* biological-physical model over past contributions is the specific spatial and organismal precautionary advice provided for marine resource managers. The authors determine that subsidies are more likely in some Caribbean regions such as the Bahamas than in others such as the Windward Islands and Mexico's Caribbean Yucatan coast, because many of the reefs in the latter regions are beyond the dispersal kernel emanating from adjacent reefs. In effect, the discontinuous distribution of coral reefs provides a network of "stepping-stones" if reefs fall within the dispersal kernel of adjacent reefs (see the figure). However, as reef habitat and its associated reproductive fish populations decline (*3*, *8*, *9*), the distances between stepping-stones may increase to the point where they exceed the larval dispersal kernel, causing connectivity to decline (*9*).



Sustaining Caribbean reef fish populations. Shrinking larval dispersal kernels and connectivity due to **(top graphs)** increased proportion of self-recruiting larvae and declining abundance of reproductive populations, and **(bottom graphs)** diminished abundance of stepping-stones within the dispersal region for larvae. Horizontal shading in top graphs represent the ecologically important number of larval recruits necessary to sustain fish populations demographically, whereas the lower, unshaded portions represent the evolutionarily important number of larvae necessary to connect populations genetically. Arrowed lines in bottom denote connectivity among populations within or between adjacent reefs. Dotted arrowed lines represent limited or sporadic connectivity. [Modified from (*9*), copyright 2005, with permission from Elsevier]

The natural-history characteristics of fish species are also critical to their sustainability in a world increasingly influenced by human activities. Whereas short-lived fish may require regular recruitment to sustain their populations, longer lived species persist with periodic pulsed recruitment events. However, fishing pressure on reefs reduces both the population density and body size of harvested species (*10*, *11*), which can, in turn, reduce larval abundance and thus shrink the dispersal kernel and effective connectivity distance (see the figure).

Although Cowen *et al.* focus on several common groups of reef fish with different larval durations and swimming behaviors, their conclusions apply to most occupants of coral reef ecosystems. Understanding what drives connectivity in these diverse ecosystems helps us to understand their resilience. For example, in recent decades, reefs suffered widespread coral mortality owing to diseases and thermally induced bleaching (*1*). However, recovery may be limited by the generally short dispersal kernels of most corals owing to their brief period of larval development while planktonic (*12*). Because some corals provide essential habitat for some reef fish (*13*), limited connectivity among corals may limit the recovery of dependent species of reef fish.

Reef management should integrate this new understanding of the geography of resilience. The Cowen *et al.* model predicts that some reefs might be more susceptible to the effects of overfishing than others elsewhere in the Caribbean. Similarly, different reef-dwelling organisms such as corals, fish, and lobsters have vastly different larval durations [that is, short (few days to weeks), medium (months), to very long (a year or more), respectively], which add to the challenge of managing these diverse ecosystems.

The growing movement toward ecosystem-based management (*3*, *14*) and for networks of unfished or "no-take" fish reserves requires that they be spaced for connectivity. The approach illustrated by Cowen *et al.* should be broadly applicable because the inputs to their models—larval duration and behavior and the physical oceanography—apply to most organisms in most marine ecosystems. Finally, as these authors point out, their model suggests testable hypotheses with specific predictions that will allow the science of ecosystem-based management to move forward adaptively (*2*).

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Extended Abstract - What Maintains the Western Gulf of Maine Cod Stock?
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Introduction

Maps of the distribution of cod, derived from National Marine Fisheries Service (NMFS) survey data, show distinct centers of cod population in the Gulf of Maine/Georges Bank region (Figure 1). Particularly high cod densities are consistently seen in the western Gulf of Maine, in the areas of Ipswich and Massachusetts Bay and Stellwagen Bank. The recent fish tagging studies of Howell et al. (2008) and Tallack et al. (2009) indicate that this western Gulf of Maine cod stock complex may be dominated by a "stay at home" group, characterized as "sedentary, resident" by Howell et al.

Genetic work of Wirgin et al. (2007) and Breton et al. (2009) has further indicated that this cod stock may be, in some respects, genetically distinct from the other cod groups in the region. The distinction, however, differs with spawning time. There are two major spawning events in the western Gulf of Maine: a spring spawning that generally occurs in May and June, and a winter spawning typically occurring over December and January. According to the genetic analysis noted above, a large fraction of the cod participating in the spring spawning genetically differ from the other spawning cod of the Gulf of Maine/Georges Bank region, whereas the winter spawning cod have genetic similarities with cod of other regions, particularly in Nantucket Shoals and the eastern New York Bight.

Although high fish densities are consistently seen in the Western Gulf of Maine, the success of cod recruitment in this area varies significantly. Population analysis conducted by the NMFS indicates that the recruitment success (ratio of newly recruited juveniles to the spawning stock biomass) of cod in the western Gulf of Maine has undergone significant variation over the past 2 1/2 decades, differing by more than a factor of 25 from a low in 2000 to a high in 2005 (Figure 2).

The spring-spawning cod population in the western Gulf of Maine thus appears to be a distinct group with limited reproductive connection with other regional cod groups. The study described here is focused on three fundamental questions regarding the cod stock of the western Gulf of Maine:

What controls the variation in recruitment success?

What maintains the western Gulf of Maine cod stock?

How did it evolve?

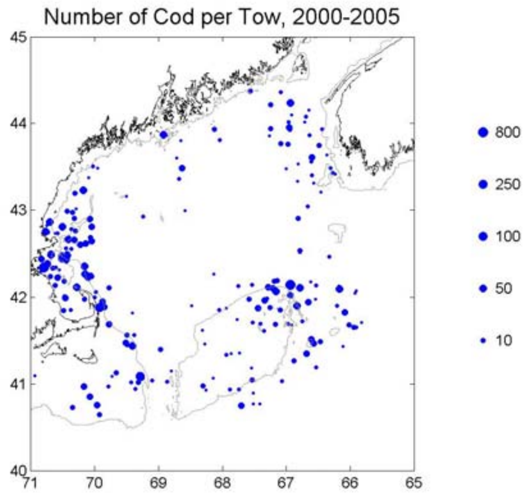

Figure 1. Distribution of cod, expressed as number of cod per tow, derived from National Marine Fisheries Service survey data acquired over 2000-2005. Note the particularly high concentration of cod in the western Gulf of Maine.

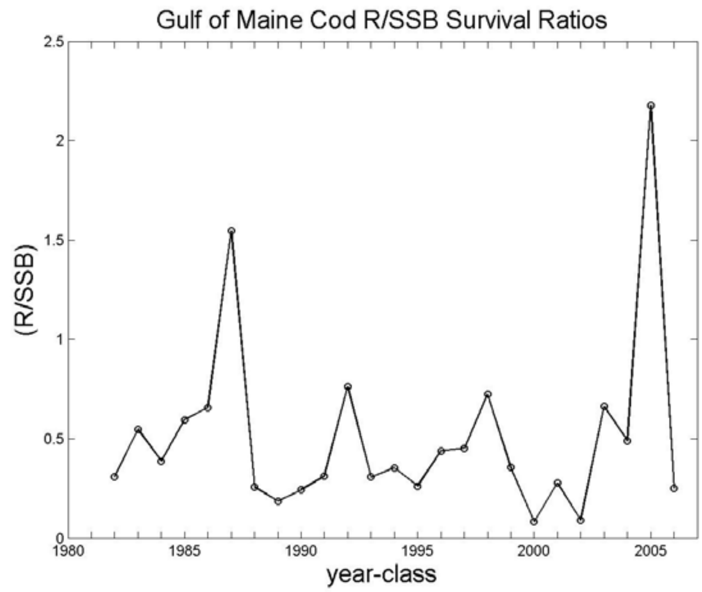

Figure 2. Year-to-year variation in survival ratios (juvenile recruits to spawning stock biomass) of Gulf of Maine cod as determine by NMSF assessments (values supplied by Loretta O'Brien, NEFSC/NMFS Woods Hole, MA)

Approach

To address these questions, we used the velocity fields generated by a hydrodynamic model of the Gulf of Maine/Georges Bank region to simulate the movement of developing cod eggs and larvae and to determine the likelihood that the larvae arrive at areas suitable for settlement as young juveniles. The model results were supplied by the Marine Ecosystem Dynamics Modeling group at U. Mass. Dartmouth (courtesy of C. Chen) and were generated by the FVCOM Gulf of Maine/Georges Bank model (http://fvcom.smast.umassd.edu/FVCOM/index.html). The velocity fields were of high resolution in both time (1 hour interval) and space (order 1 km cell size in the coastal zone).

Our focus was on cod spawned in Ipswich Bay (Figure 3) during the spring spawning event. In carrying out the modeling, the newly spawned cod eggs were assumed to be buoyant and to reside in the near surface layer of the stratified water column, subject to direct forcing by the surface wind stress. The manner in which larval transport is impacted by diel vertical migration of larvae was also examined, as detailed below. The age of settlement capability was assumed to be in the range of 45-60 d (e.g. all cod were assumed to settle by an age of 60 days). Based on the distribution of age-0 juvenile cod reported by Howe (2002), the western Gulf of Maine region suitable as an early stage juvenile habitat was taken as the coastal area with depth of < 30 m.

In carrying out the transport simulations, ensembles of cod eggs distributed over the Ipswich Bay spawning region were released into the modeled flow field at intervals of 3 days over May and June. Each developing cod egg/larvae particle was tracked for 60 days. From the tracks, we determined the ensemble likelihood that the drifting cod arrive at a settlement suitable area at an age when settlement capable, a quantity defined as transport success by Huret et al. (2007). This was taken as the percent of time that particles (larvae) of the ensemble were over depths of less than 30 m (i.e. in a region suitable for settlement) during the last 15 days of their 60 day drift (i.e. the assumed age of settlement capability). The transport success was averaged over ensembles giving an expected success of transport to settlement areas for releases (spawns) during a given time period.

Transport simulations were carried out over 11 spring spawning events, from 1995 to 2005, and the resulting year-to-year variation in computed transport success was compared with the wind, measured at the NOAA 44013 weather buoy in Massachusetts Bay (Figure 3).

Understanding the relationship of wind to transport success requires knowledge of the large scale Gulf of Maine circulation. Numerous studies have shown that this circulation is dominated by a current that flows counterclockwise about the Gulf of Maine Basin. It is referred to as the Maine Coastal current, although this is somewhat of a misnomer as it is not bound to the coast but typically centered near the 80-m isobath. In the western Gulf of Maine, it takes the form of the Western Maine Coastal Current (WMCC), which flows southward off the coast of Massachusetts (Figure 4).

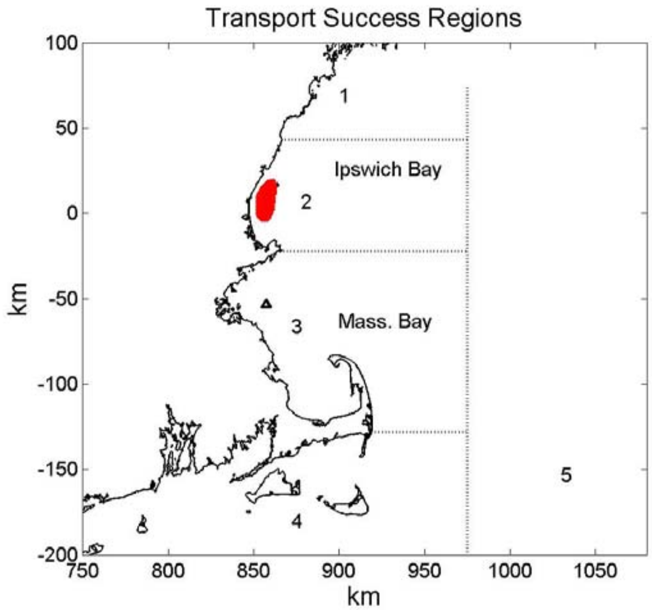

Figure 3. Our study region. The red area encompasses our representation of the Ipswich Bay spring spawning area from which ensembles of particles, representing developing eggs and larvae, were released into a modeled flow field. Success of larval transport to suitable settlement area of regions 1-5 was computed from the simulated egg/larvae tracks. Our focus is on transport success to regions 2 and 3. Because of the mean circulation in the Western Gulf of Maine, transport to region 1, north of the spawning area, was negligible. The triangle in region 3 marks the location of the NOAA 40013 weather buoy.

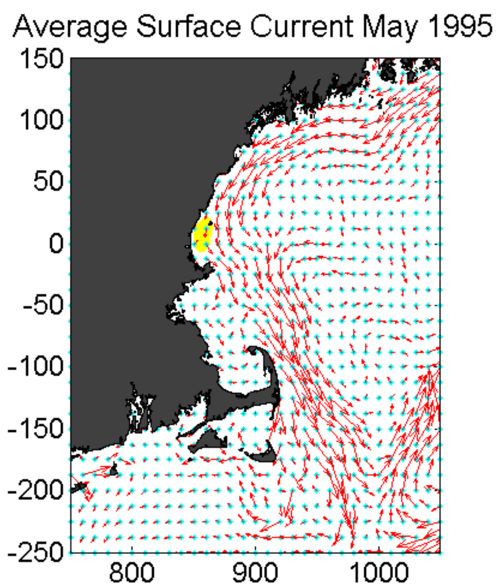

Figure 4. An example of the modeled flow field generated by the Gulf of Maine/Georges Bank FVCOM model. The vectors are average surface currents for May 1995. As the mean wind in May 1995 (measured at buoy 44013) was nearly zero, these currents are the modeled representation of the non-wind driven flow field in the western Gulf of Maine. They show the strong southward flow of the Western Maine Coastal Current bypassing Ipswich and Massachusetts Bays.

Results

To best understand the effect of wind on egg/larval transport, we first consider the movement of particles released at the Ipswich Bay spawning site and confined to the near-surface (wind-driven) layer (i.e. ignoring diel vertical migration in the larval stage). The yearly-averaged transport success of such particles to the Massachusetts and Ipswich Bay regions (regions 2 and 3 in Figure 3) shows considerable year-to-year variation (Figure 5).

To explore how wind forcing of the ocean surface layer may be responsible for this variation, it is necessary to understand the manner in which wind affects the surface layer current in terms of upwelling (with the surface layer flow directed offshore) and downwelling (with onshore surface flow). In Massachusetts and Ipswich Bay, a westward wind (from the east) will tend to generate on onshore flow and is thus downwelling favorable. Conversely, an eastward wind is upwelling favorable. Because of the effect of the earth's rotation, a southward wind in Massachusetts and Ipswich Bay region will force the surface layer westward and is downwelling favorable, whereas a northward wind tends to force upwelling.

Comparing the transport success of fixed-depth particles with the wind velocity averaged over each May (Figure 6) shows that the transport success to Massachusetts and Ipswich Bay tends to be high for those years when the averaged May winds are downwelling favorable. The reason for this is simple. Upwelling circulation tends to carry buoyant particles originating in Ipswich Bay offshore towards the WMCC, which transports the particles rapidly out of the region. Conversely, downwelling circulation tends carry particles onshore, allowing them to remain in the Ipswich Massachusetts Bay region, isolated from the WMCC. This same mechanism is responsible for a difference in the transport success of May vs June particle releases, with the transport success of the May releases being significantly higher than the transport success of the June releases (not shown). This is the result of a May-to-June shift in the wind pattern in the Western Gulf of Maine which results in predominantly upwelling favorable winds during each June of the years considered in our modeling (1995-2005).

Surprisingly, the introduction of diel vertical migration during the larval stage (migration to the surface at night for feeding and to depth during the day to avoid predators) has only moderate effect on the year-to-year variation in transport success to Ipswich and Massachusetts Bay as determined by our simulations. In general, the yearly-mean transport success is increased slightly with the introduction of vertical migration in the larval stage (Figure 7). The reason for this enhancement relates to the impact of upwelling circulation on those larvae that are within Ipswich and Massachusetts when they become capable of migration (at 3 weeks after spawning in our simulations). If these larvae remain fixed at the surface during an upwelling event, they will tend to be carried offshore towards the WMCC. However, with vertical migration, the larvae will be at sometimes within the lower layer and carried onshore. The net effect will be compensating onshore and offshore jogs for the vertical migrating larvae during the course of a day, as opposed to the persistent offshore movement that larvae confined to the surface layer will experience during upwelling circulation.

With or without diel migration included in the transport simulations, the estimated success of larval transport to settlement suitable area of Massachusetts and Ipswich Bay is fairly well related to the cod recruitment success for the western Gulf of Maine as estimated by the NMFS (Figure 5). In particular, years of high recruitment success (1998 and 2003) are also years of high transport success according to our simulations.

The results of our simulations suggest that the mean wind of May may be used as a predictor of recruitment success of cod in the western Gulf of Maine, specifically that an average May wind which is downwelling favorable might indicate conditions favorable for recruitment. Comparing the mean May north-south wind with the estimated recruitment success for the 1985-2005 period indeed indicate such a relationship. Recruitment success is particularly high in those years in which the mean May wind (measured at buoy 44013) is downwelling favorable (Figure 8). Most notable is 2005, which has both the highest recruitment success and the most strongly downwelling favorable wind during May for the 1985-2005 period.

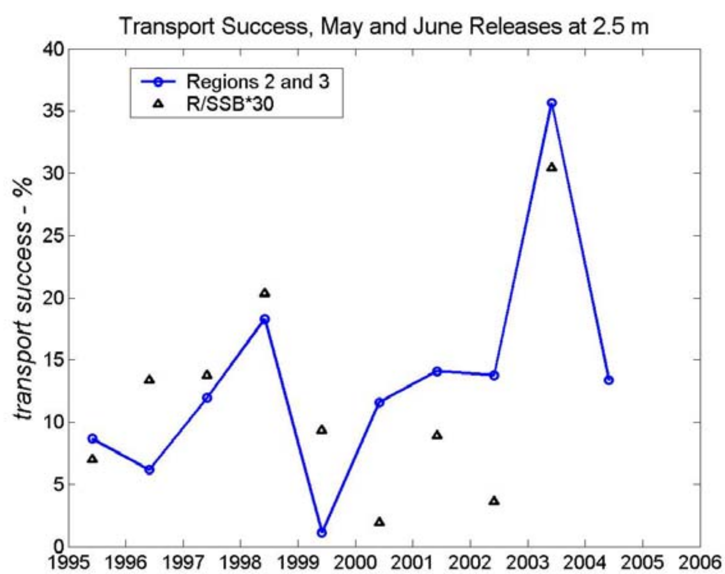

Figure 5. A comparison of recruitment success of Gulf of Maine cod determined from catch and survey data by the NMFS (triangles) with the success with which spring-spawned cod are transported from the Ipswich Bay spawning area to settlement suitable areas in Ipswich and Massachusetts Bay (blue line). The transport successes are for the case in which the developing eggs and larvae are held at a fixed depth during the transport simulations. Note a fair correlation between the transport and recruitment success values.

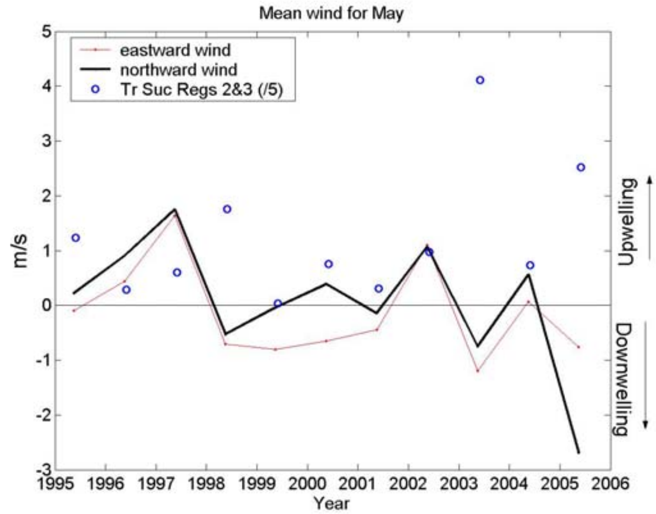

Figure 6. Comparison of the estimates of transport success to the Ipswich and Massachusetts Bay regions with the mean wind velocity of May measured at NOAA buoy 44013 (Figure 3). Note that the estimated transport success is always high when the mean wind of May is downwelling favorable.

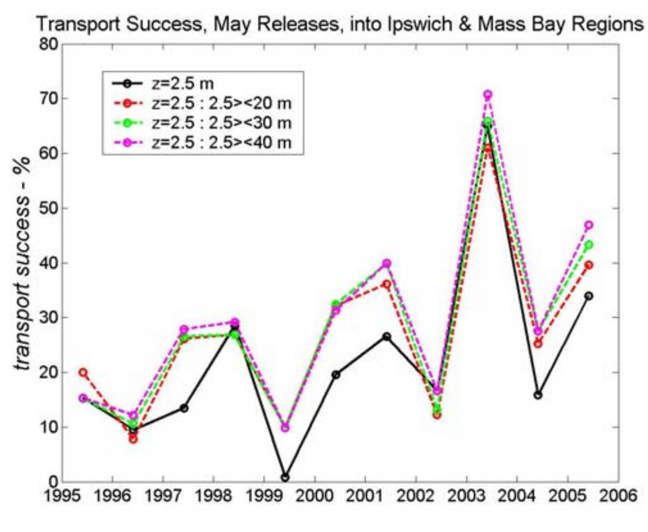

Figure 7. Comparison of the success of larval transport to settlement suitable area in Ipswich and Massachusetts for particles fixed at 2.5 m depth (black line) and particles which undergo diel vertical migration in the larval stage (colored lines). The depth limits of the migration are indicated in the legend.

Figure 8. Comparison of the recruitment success of cod in the western Gulf of Maine with the mean north-south wind velocity of May measured at NOAA buoy 44013 (Figure 3). Note that the recruitment success is largest during those years when the mean wind of May is downwelling favorable (directed to the south)

Summary

The analysis reviewed above supports the following conclusions:

Coupling of wind-driven near-surface transport with the larger-scale Gulf of Maine “Coastal Current” controls whether Ipswich-spawned cod eggs and larvae are retained in the western Gulf of Maine or broadcast to distant areas (downwelling winds are larval retentive; upwelling winds are larval broadcasting).

The fate of the larvae is largely cast by the wind-driven transport in the buoyant egg stage, with diel vertical migration marginally enhancing retention.

Recruitment success in the western Gulf of Maine may be largely tied to the retention of the May-spawned population

Hypotheses

Coupled with the recent findings of the genetic and tagging studies mentioned in the Introduction, the results presented here also lead to some interesting hypotheses regarding the impact of cod spawning in the western Gulf of Maine. Three hypotheses, which may be particularly useful in guiding future studies, are:

The two spawning times strategy. It is possible that two spawning events in the western Gulf of Maine be part of different population strategies. The spring spawning may principally serve in sustaining the local western Gulf of Maine cod population, characterized as resident, sedentary by Howell et al. (2008). By contrast, the winter spawning may be important in supplying recruits to a more broadly dispersed cod complex, including Nantucket Shoals and the eastern New York Bight. This is consistent with the analysis of genetic markers by Wirgin et al. (2007) and Breton et al. (2009), which indicates that the cod spawning in Ipswich Bay during spring are genetically distinct from other regional cod stocks, whereas cod spawning in the western Gulf of Maine in winter are genetically similar to cod of other regions, particularly in Nantucket Shoals and the eastern New York Bight

The sedentary-resident population is sustained in Massachusetts Bay because it’s a pocket isolated from the WMCC. The stay-at-home cod population of Massachusetts and Ipswich Bays may be maintained partly because these areas are largely isolated from the WMCC and thus are zones of larval cod retention.

Ipswich Bay evolved as a prime spawning local because it is upstream of the Mass Bay pocket. The aggregation of spawning cod in Ipswich Bay during spring may have evolved because of two factors. Ipswich Bay is uniquely situated at the “upstream” extreme of a larval retentive area, isolated from the WMCC, and the wind and water column stratification conditions during spring (particularly May) are ideal for retaining eggs and larvae in this region.

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