

Progress to date: Effective management and conservation of Canada's living marine resources requires an understanding of the linkages among different populations. However, spatially-explicit population models for fish populations have been difficult to generate, because the ocean is vast and most marine species produce many propagules whose dispersal potential is usually poorly documented¹. Recent applications of metapopulation theory to marine fish species² provide a framework for exploration of the importance of exchange and dispersal for marine. A meta-population is a set of local populations in a larger geographic area with possible movement between local populations³. '*Population connectivity*' defines the degree to which one or more populations exchange individuals. Understanding connectivity between populations is fundamental to successful fisheries management and to conserve biodiversity of threatened populations. Establishing sources and sinks for reproductive propagules in ocean systems is critical to designing effective marine protected areas and recovery strategies for threatened species⁴.

Despite their importance, connectivity measures have proven elusive. Recent advances in molecular genetic markers⁵ and geochemical signatures in calcified structures⁶⁻⁸ have enhanced marine dispersal studies, and quantified population connectivity with varying resolution. Traditional genetic approaches measure dispersal and connectivity using unrealistic population models and assumptions⁹. These approaches estimate number of migrants (N_m) based on genetic differences among subpopulations (e.g., F_{st}) using simple models of gene flow, resulting in estimates that may vary by orders of magnitude from reality¹⁰. Recent successful alternatives to traditional approaches have utilized genetic isolation by distance relationships (IBD^{10,11}) or assignment testing¹² of multilocus genotypes¹³⁻¹⁴. Geochemical signatures in otoliths (fish ear bones) have been especially useful in describing self-recruitment where subpopulations are not genetically distinct yet mostly segregate ecologically^{16,17}, and complements genetic approaches. Together these tools provide critical data on evolutionary and ecological time scales that are both relevant to fisheries management.

Despite advances in tools necessary for quantifying connectivity, there has been little effort to embed such techniques in a mechanistic framework for use in marine systems. Dispersal theory and population connectivity in terrestrial species has typically been examined in the context of habitat landscapes¹⁸ and species life history. By incorporating the spatial distribution of habitat (patches, corridors) with measures of life history dispersal potential¹⁹, terrestrial ecologists have successfully described how metapopulations persist across their geographic range²⁰. Terrestrial studies can track individuals and categorize habitat types more easily. In contrast, most marine fish possess multiple dispersal phases (e.g. larvae, adults). Therefore landscape approaches have not been undertaken in marine systems. Estimates to date integrate over the entire life history^{16,21} and do not identify critical stages or habitats.

We propose to develop landscape models to quantify connectivity at multiple scales and life history stages of marine organisms. These models will incorporate empirical field data (physical and behavioural), genetics, otolith microchemistry, and habitat distribution to examine how life history helps subpopulations persist. Such models will delineate the appropriate spatial and temporal (i.e., life stage) boundaries necessary for conservation and recovery. To demonstrate our approach and explore life history influences on connectivity, we will study three marine fish species residing in coastal Newfoundland with contrasting dispersal potential (shorthorn sculpin - winter spawner, demersal eggs; Atlantic cod - spring spawner, pelagic eggs; and rainbow smelt - anadromous spring spawner, demersal eggs). Coastal zones (0-50km offshore) and bays support most of the remaining biomass of demersal fishes in Newfoundland, yet the connectivity of these populations within and between bays is unknown. Our work is timely given ongoing development in the coastal zone (oil, aquaculture) and recent concerns regarding several marine species (e.g. the northern population of Atlantic cod has been listed as "endangered" by COSEWIC, the Committee on the Status of Endangered Wildlife in Canada).

Objectives: Our project has six objectives that focus on five large eastern Newfoundland bays: Bonavista, Trinity, Conception, St. Mary's and Placentia (Fig 1), and will determine:

- 1) Spatio-temporal egg and larval distributions within Trinity Bay for cod and the full survey area for smelt and sculpin
- 2) Oceanographic connections between bays, within Trinity Bay
- 3) Juvenile fish usage of patchy habitats
- 4) Spatio-temporal patterns of movement from larval through juvenile stages though the full survey area
- 5) Connectivity mechanisms of populations within bays (modelling, juvenile tagging) and among bays (otolith microchemistry, genetics)
- 6) Full connectivity models of larvae, juvenile, adults & habitat.

Literature Review: Effective management of biological metapopulations requires data on spatial habitat use. However, establishing dispersal potential and connectivity among aggregations of individuals utilizing critical habitat is also important. But estimates of marine local recruitment are rare²² and fall short of full-scale dispersal models. Terrestrial ecologists have developed mechanistic models of aggregation connectivity^{18,23} that highlight dual roles of habitat structure²⁴ and organism movement²⁵ in ecological connections. New models based on graph theory²⁶⁻²⁸ present a means of integrating metapopulation processes with landscape pattern, and could help to develop mechanism-based measures of connectivity in marine systems. Such models accommodate both organism movement and habitat structure²⁸, thereby allowing *integrated* connectivity estimates. In these models, each metapopulation is represented by a node; in landscapes, nodes represent discrete areas of habitat or organisms (Fig 2). Pairs of nodes are joined by edges that represent a binary relationship between the two nodes; often a weight or cost factor, such as a functional distance (e.g. dispersal

probabilities, mortality rates), is assigned to edges between nodes. Such models then enable graph-theoretic concepts and heuristics to be applied: minimum weight spanning trees indicate the connectivity between populations, cut nodes indicate habitats critical to sustaining connectivity between populations, and cliques and other densely-connected groups of nodes can reveal metapopulations that can be treated as a single management unit. Sub-population persistence within a meta-population can also be studied by means of node and edge removal analyses. Thus, Graph Theory can assess sub-population persistence within a metapopulation. This approach will significantly improve our understanding of marine dispersal, which is often defined as loosely defined exchange within a patchy matrix of larval sources/ sinks, and ill-defined habitat.

In Newfoundland, much of the remaining biomass of demersal fish species resides inshore following intense offshore fishing³⁰. Many of these species are candidates for protection following rapid declines in abundance (e.g. Atlantic cod, shorthorn sculpin). Our data on localized recruitment in Atlantic cod (Fig 3) indicate a need to re-evaluate past management strategies that are based on geographic lines rather than solid biology. In light of population declines and the mismatch between scales of management and ecology, better spatial biology of coastal fish populations is needed.

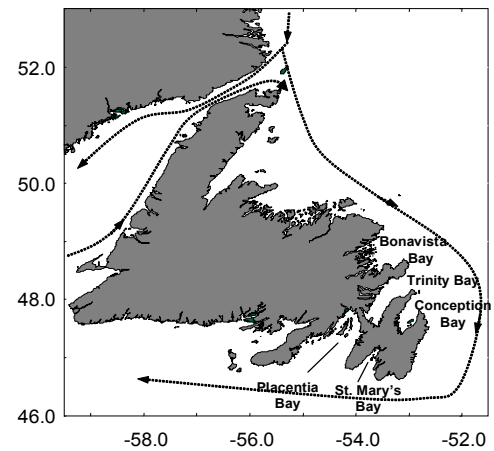


Fig. 1. Schematic of Newfoundland showing the five bays that will be sampled. Arrows show broad-scale circulation.

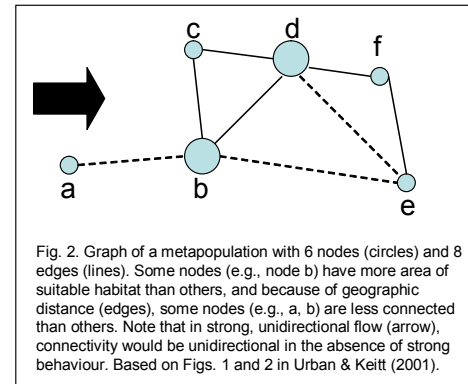


Fig. 2. Graph of a metapopulation with 6 nodes (circles) and 8 edges (lines). Some nodes (e.g., node b) have more area of suitable habitat than others, and because of geographic distance (edges), some nodes (e.g., a, b) are less connected than others. Note that in strong, unidirectional flow (arrow), connectivity would be unidirectional in the absence of strong behaviour. Based on Figs. 1 and 2 in Urban & Keitt (2001).

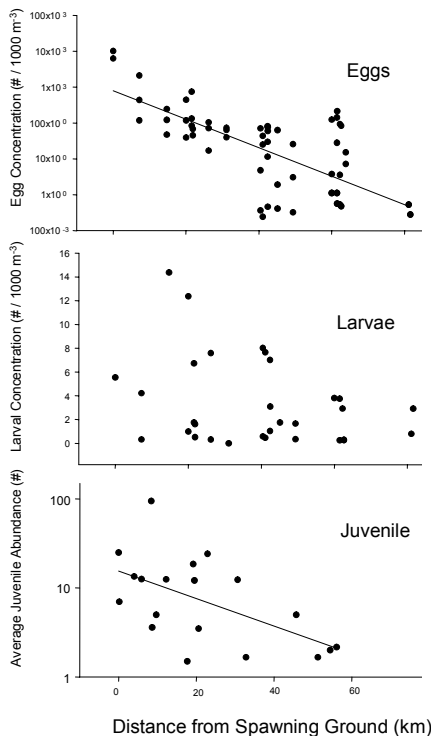


Figure 3. Evidence of self-recruitment in Atlantic cod. Abundance with distance from spawning area in Placentia Bay from surveys in 1997-1999 (Bradbury et al. unpubl.)

Methods and Proposed Approach: We propose to determine landscape connectivity for larval and juvenile stages of northern cod, shorthorn sculpin and rainbow smelt using models based on graph theory for coastal Newfoundland at multiple spatial scales. Larval, juvenile and adult patches (i.e. nodes) will be determined using traditional net sampling techniques. Larval and adult habitat will be defined in relation to water mass characteristics. The functional distance between nodes (i.e., larval_i-larval_j, larval-juvenile, juvenile_i – juvenile_j and juvenile-adult connections) will be based on dispersal/movement probabilities resulting from interactions between habitats, internodal Euclidean distance, and fish behaviour and mortality. Our predictions of between-bay connectivity using models based on graph theory will utilize biophysical modelling of larval-juvenile linkages, whereas for juvenile-adult linkages we will use elemental signatures in otoliths and genetics of juvenile and adult fish sampled from each bay. We will examine environmental exposure as a function of habitat from trace element composition using lab rearing to verify trace element integration in relation to salinity and temperature³¹.

Connectivity will be determined from two sets of data: one describing the nodes (i.e., habitat patches) and one describing the edges (functional inter-nodal distances). Nodes are defined by their spatial centroid (x,y) and a quantitative descriptor (s) referring to either its size, productivity, quality, etc. Nodes (x,y,s) will be defined for inshore larvae, nearshore (<1 km, neuston survey, see below) larvae and juveniles in each species. Edges will consist of a functional distance matrix **P** of components f_{ij} that define the distance between nodes *i* and *j*. The general dispersal flux equation that will calculate

functional distance between each node pair is defined as: $f_{ij} = \frac{S_i}{S_{tot}} \times p'_{ij}$ where *s* = size of the habitat

patch and *p* is the dispersal probability from *i* to *j* normalized by *i*'s row sum in its dispersal matrix **P**. Because $f_{ij} \neq f_{ji}$ (e.g. upstream vs downstream movement, unidirectional flow between larvae and juvenile nodes), we will incorporate an area-weighted flux w_{ij} for each node pair such that:

$w_{ij} = w_{ji} = 1 - \frac{f_{ij} + f_{ji}}{2}$. For each species, edges will be constructed between larvae-larvae, larvae-

juveniles, and juveniles-juveniles. In a practical sense, we consider populations connected if sufficient numbers of successful recruits are transported *per generation* between subpopulations to significantly influence population numbers (e.g. 20%). Estimates of proportional composition of populations will be based on otolith signatures. Our hypotheses include:

Hypothesis 1: Cod connectivity is high among adjacent bays, but not between coasts. Connectivity between bays is via pelagic egg/larval/adult movement and within bays by larvae/juveniles.

Hypothesis 2: Smelt connectivity will be lower than cod because of demersal eggs and active larval retention. Within-bay structure exists (i.e. each estuary); any connectivity is via adults.

Hypothesis 3: Sculpin are intermediate in connectivity relative to cod and smelt. Demersal eggs with pelagic larvae suggest high within-bay but low between-bay connectivity given restricted adult movement. We predict differences between but not within bays.

Goal 1: Spatial-temporal distribution of larvae patches. Given contrasting life history strategies, we will approach each study species somewhat differently. We will focus on Trinity Bay; cod aggregate in Smith Sound (Fig. 4) to spawn, producing pelagic eggs with wide dispersal potential. Relatively high-frequency ring net plankton sampling (e.g. twice per week) in Smith Sound will therefore allow us to (1) identify times when larvae are likely to be present by forecasting development trajectories, and (2) try to identify pulses (cohorts) which we can then link to subsequent juvenile spatial patterns, again by projecting development times forward³² but also by linking to the hydrographic model (see below) to estimate spatial

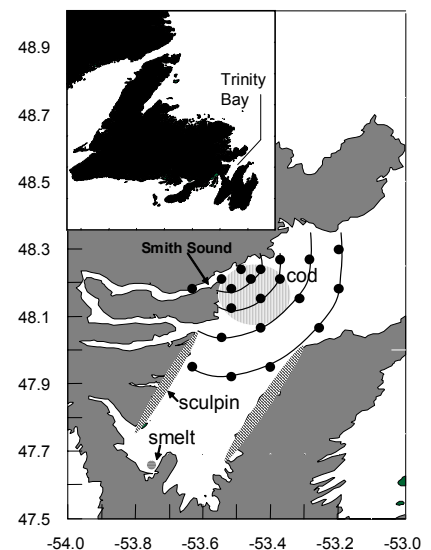


Fig. 4 – Main spawning sites for focus species. Note contrast in geographic extent of spawning activity and possible sources of propagules. Solid lines denote expanding bullseye grid for egg/larval sampling; dots are stations occupied in 2004.

dispersal. This approach will determine the larval fish node (s_{larvae}) size and spatial-temporal distribution. During periods of high larvae abundance (e.g. June³⁶), we will then conduct two consecutive larval surveys with adaptive sampling working away from Smith Sound with decreasing spatial resolution (Fig. 4) using oblique 2m x 2m Tucker trawls to 40 m depth¹² at ~17 stations. A back-to-back survey design can quantify patch movement of recently-hatched larvae to test the physical model predictions. Each survey will require ~2 days. We will also collect neuston samples at the juvenile survey sites (see below) in mid-September and early October to estimate concentrations of late stage larvae. These data will document spatial shifts in late stage larvae and link larval supply to juvenile abundance. Although we will not sample the full cod (or other taxa) larval phase (expensive, likely unsuccessful, and would require multiple sampling gear surveys), we will evaluate patch dispersal trajectories from Smith Sound, move them forward with our circulation model and estimate how larval transport influences within-bay connectivity. We will deploy several acoustic Doppler current meter moorings at key areas to provide Eulerian measurements of currents to provide data on intermittent forcing that advects and disperses³³. Mooring data will be used to test and initialise the circulation models. Ship support from DFO in 2004 provided preliminary data that will guide efforts in 2006-7.

Larval smelt are confined to coastal estuaries in their first year^{34,35} and are not caught in coastal larval tows^{36,37}. Smelt concentrations and sites of s_{larvae} will be determined with 1 x 2 m neuston net tows at juvenile sites (see below) and Trinity Bay estuaries in mid-June/July when smelt larvae (and shorthorn sculpin) are abundant (Fig. 5). As with cod, paired surveys can address distribution shifts among sites.

Shorthorn sculpin spawn along strips of shoreline habitat (Fig. 4). Estimated s_{larvae} and spatial distribution for sculpin will be determined with neuston nets as described above. Given the weak coastal currents in much of Trinity Bay and their demersal, nearshore spawning strategy, we predict that larval dispersal will be much less than for cod but greater than for smelt. For all samples, eggs and larvae will be staged and measured respectively; size data for larvae are key elements for the coupling model.

Goal 2: Oceanographic connections within& between bays - Larval fish dispersal probabilities ($p_{larv_i-larv_j}$). We will use ichthyoplankton data to examine dispersal using two approaches. First, we will use back-to-back surveys to determine shifts in distributions of eggs (passive null model) and larvae (limited behavioural component possible) of sequential stages and sizes between the two surveys³⁸. Larval fish dispersal probabilities ($p_{larv_i-larv_j}$) will be determined using frequency distributions generated by combining local current flow observations (B. deYoung) with results from a prognostic circulation model³⁹ of node concentrations of larvae from larval fish surveys. We have all the components of a larval life history model prepared for inclusion in the circulation models with which we also have substantial experience. We will follow an approach of applying the level of biological detail necessary to address the key problems⁴⁰. Models will be run for the duration of the larval period (~40 d) to determine the resulting “source” and “sink” patterns and corresponding nodal connectivity ($s_{larv_i-larv_j}$). We can look at size progression within a survey and assume that larger individuals have dispersed for a longer time period than smaller individuals. deYoung’s model will be used to hindcast initial distributions of larger individuals to compare with the distributions of smaller individuals and late stage eggs (i.e. larval “sources”) at earlier dates. Moreover, an MSc student in Snelgrove’s lab is currently conducting flume experiments to determine larval swim speeds at different developmental stages for cod and sculpin; these data will add a behavioural component to deYoung’s model. We will seek similar data for smelt. For cod, this approach will be strengthened with ring net sampling to identify Smith Sound spawning pulses. Surveys in Yr 1 and 2 will document interannual variability. We will also use larval development times and circulation models to estimate connectivity potential between bays. We predict this approach will show larval connectivity between adjacent bays but not between the north and south coasts.

Goal 3: Juvenile fish nodes (s_{juv}): Spatial-temporal distribution of juvenile patches. Juvenile fish patch structure will be determined in coastal areas in each bay. Juvenile fish will be sampled with a demersal beach seine at eelgrass sites delineated by habitat maps developed in Arc/Info (see below). However, we expect that many of these sites will overlap with sites used for previous sampling of

demersal juvenile fish in these bays^{4,42}. The seine captures juveniles of all the proposed study species with 95% efficiency⁴³, can be deployed by two people in a small boat, and samples an effective seabed area of 880 m². Sampling will occur in mid-September and will be conducted by two seining teams operating simultaneously in separate bays to minimize any confounding seasonal effects. Sampling will occur in Year 1 and 2 using small boats provided by DFO. Additional juvenile fish needed for otolith microchemistry and genetics will be collected and preserved during the survey in Year 1, but impact will be minimized since the beach seine is non-lethal and most fish can be returned alive to their capture site.

Goal 4a: Larval-juvenile fish dispersal flux ($p_{larv-juv}$). Dispersal flux between larvae and juvenile habitats is a function of both larval supply and habitat selection by larvae⁴⁴⁻⁴⁵⁴⁴. These mechanisms are both important. Therefore we will summarize them in the form of a negative-exponential decay equation, $p_{larv-juv} = \exp(\theta \times d_{larv-juv})$ where θ equals the distance-decay coefficient for a given patch (node) and d equals the Euclidean distance separating nodes of larvae and juveniles. We will determine θ by examining signal-to-noise ratios (t-ratios) of larval and juvenile concentrations with increasing geographic distance from one another⁴⁶ at scales ranging from 50 - 10000 m in each bay. Larval concentrations will be determined via alongshore neuston sampling in August at juvenile sampling sites.

Goal 4b: Juvenile-juvenile dispersal flux($p_{juv-juv}$). Along-coast flux of juveniles between nodes will depend on habitat distribution between nodes and fish behaviour in response to habitat distribution. The former will be determined using existing models⁴⁷, which combine spectral properties of habitat type from remotely sensed images (LANDSAT 5 25m x 25m) with physical predictors of those habitat types (e.g. exposure). Since 1999, satellite images have been available at higher resolution in our study area (Landsat 7, 15 m x 15 m resolution) Habitat will be ground-truthed with high-precision differential GPS at multiple locations⁴⁸. Maps will be constructed by DFO GIS specialist N. Ollerhead in Yr 1.

Behavioural experiments on juvenile fish will be conducted in Years 1 and 2 in Terra Nova National Park in Newman Sound, Bonavista Bay in order to determine the habitat gap-crossing abilities of each of the focus species. The probability that a juvenile fish will move between habitat patches is expected to be negatively related to between-patch distance, but is likely species-specific and may vary between linear to threshold responses⁴⁸. To determine among-habitat movement for each species, we will deploy two 30 m² patches of artificial eelgrass (wired grids and ribbon⁵⁰⁹) 500 m apart at a sandy beach devoid of eelgrass. Fish of each species collected nearby at productive eelgrass areas will be marked using a fluorescent grit marking technique⁵⁰ or similar approach suitable for batch marking of large numbers of fish. Marked fish will be released at fixed distances from patches (0, 50, 100, 500, 1000 m) and recaptured by beach seine at 1-day intervals at each patch. Use of different colour grits for each distance will allow simultaneous recapture effort at all intervals. Recaptured fish will not be returned to study areas. This design allows us to assess mortality, movement, and asymmetric transfer among patches⁵¹⁸.

Goal 4c: Juvenile-adult dispersal flux ($p_{juv-adult}$), large-scale between bay connectivity. We will use genetics and otolith microchemistry to evaluate connectivity among fish populations from five Newfoundland bays (Fig. 1). Selection of trace elements for analysis will be based on three criteria: 1) the element is free of significant interferences that cannot be resolved by high resolution LA-ICPMS (Laser Ablation Inductively Coupled Plasma Mass Spectrometry), 2) the element has been sampled in coastal environments and varies geographically in our sampling region, and 3) the element is incorporated in fish otoliths in proportion to environmental concentrations and conditions. Analyses of multiple species have shown that many trace elements are concentrated in otoliths, including Al, Ba, Cd, and others^{8,52,53}. Otolith studies suggest that Mg and Sr may be useful tracers of water mass residency¹⁶.

Distinct elemental signatures (fingerprints) for each study site (i.e., bays, nurseries) will be determined by collecting and analyzing fish from each site. Analyses will identify unique elemental fingerprints of otoliths from each site. Distinct signatures will be compared with elemental fingerprints of otolith primordia of both sub adult and adult spawning fish to determine dispersal¹⁷ Laser ablation microchemistry allows analysis of distinct regions of otoliths; differences in elemental composition of

different regions (larval (pre-hatch) zone, juvenile, adult rings) may result from movement between water masses. Thus, analytical transects across each otolith may provide a record of fish movement between water masses. However, interpretation of various elements requires that we rear juveniles under different salinity and temperature regimes at MUN. Correlations between elemental composition and lab treatments will then allow back calculation of environmental history of fishes collected from the field.

To increase the likelihood of finding distinct elemental fingerprints, species were chosen to maximize variation in hydrographic exposure either through population level migration plasticity (rainbow smelt), or through dynamic coastal nursery habitats (cod, shorthorn sculpin). For example, smelt utilize a variety of nursery habitats from freshwater ponds to partially barred estuaries. This variation should allow the use of strontium to track nursery habitats¹⁶. Likewise, cod and sculpin spawning is often near freshwater inflows (e.g. Placentia Bay spawners), and should also provide a natural elemental tag that may vary with estuarine characteristics. Thus, adults in these areas (i.e., s_{adult}) will be sampled using a combination of beach seine (smelt and sculpin) and annual DFO sampling. Given adult cod mobility, we believe that between-bay scale sampling will suffice for this species. All elemental analyses will be conducted at the Pacific Centre for Isotopic and Geochemical Research (PCIGR) using High Resolution ICP-MS (HR-ICP-MS) (Thermo Finnigan ELEMENT2) and patterns quantified using standard statistical techniques¹⁷. The elemental fingerprint will be supplemented with an analysis of stable isotopes of oxygen, strontium, and sulphur, which may further enhance the resolution of this technique.

Goal 4d: Adult-Adult, large-scale between bay connectivity. We will use multilocus microsatellite genotypes in conjunction with observed patterns in genetic isolation by distance and assignment testing, to evaluate connectivity and dispersal between the five bays. IBD approaches utilize the slope of the isolation by distance regression in conjunction with a realistic model of gene flow (i.e. one dimensional stepping stone) to estimate dispersal distances¹². In contrast, recent assignment-test based approaches utilizing highly variable nuclear markers (i.e., microsatellites) in conjunction with new statistical tools¹³ have resulted in near real time estimates of dispersal in natural populations¹⁴. Individual-based assignment tests utilizing multilocus genotypes to assign individuals to a population of origin have the potential to replace mark-recapture studies in many systems^{13,15}. An obvious limitation of probabilistic assignment is that success will increase with subpopulation isolation, paradoxically making assignment most accurate when dispersal is low. In contrast, IBD approaches have proven successful in marine species where gene flow is expected to be high¹². Suitable tetranucleotide microsatellite loci have previously been developed for Atlantic cod⁵⁴, and smelt⁵⁵, and will be developed for short-horned sculpin as part of this study at the Marine Gene Probe Lab (MGPL) at Dalhousie University, Halifax. Samples consisting of small fin clips from 100 individuals per species per bay will be removed from spawning fish and stored in 95% ethanol. DNA extractions⁵⁶, amplification, and further analysis will be carried out at the MGPL. Genotype data from all samples will be used to calculate allele frequencies and produce IBD relationships. Selection of loci for assignment will be based on preliminary screening for population-specific alleles (PSA⁵⁷) may allow for maximization of numbers of fish genotyped. Individuals will be assigned using both a Bayesian⁵⁸ and partial Bayesian⁵⁹ approach. Although these estimates do not calculate dispersal directly, an estimate may be obtained from the ratio of migrants to residents. A direct estimate of immigration will be calculated using a method⁶⁰ that relaxes the assumption of Hardy-Weinberg equilibrium, and provides uncertainty estimates of dispersal values.

Goal 5: Connectivity using Graph Theory. We will use sampling, modelling and/or experimental approaches to provide graph theory inputs for each life history stages (using genetics for evolutionary dispersal, modelling for potential dispersal, and tagging experiments and otoliths for realized dispersal within a habitat context. Each approach has its strengths; graphs of straying based on otolith data, while sensitive to high levels of mixing, do not measure dispersal success, whereas graphs using the genetic IBD and assignment tests will predict successful dispersal on evolutionary time scales. Each dataset, modelled as a graph, will be examined for its *minimum spanning tree* (shortest length connecting all nodes without cycling back upon itself). In this form, the relationship graphs can be quantified in terms of connectivity by node and edge removal methods. Edge removal iteratively deletes edges at varying

threshold distances (e.g. 20, 10, 5, 1 km) and plots threshold distance against number of remaining nodes, overall graph diameter, and total remaining graph components. The asymptote in these plots indicates the scale at which a given population becomes disconnected and vulnerable to expatriation through disturbance or overharvesting²⁶. We will use node removal analysis²⁸ to indicate how habitat loss affects overall dispersal potential and landscape traversability. Nodes will be iteratively removed in each species graph and remaining nodes will be plotted against total flux ($1/f_{tot}$) of the graph and overall graph diameter, thus delineating critical areas for dispersal and persistence.

How the landscape facilitates dispersal relates to straying rates among populations, which can be estimated within bays with biophysical modelling. At the among-bay scale, otolith microchemistry will measure straying rates from nursery areas, which can then be matched against the graphical maps. Assignment of fish to individual bays based on trace elemental composition will then establish an exponential decay curve describing dispersal (including dilution and predation) from each bay. With bays as nodes, and dispersal probabilities as edges, edge and node removal may then be compared between landscape/habitat-predicted and otolith and genetic-predicted graphs, allowing independent contrasts of the role of habitat structure in connectivity on ecological and evolutionary time scales. Graphs will give us key information to integrate and reconcile habitat and life history data. Trimming and node pruning of habitat graphs will help to link habitat and dispersal, and iterative trimming of nodes of habitat and life history graphs will clarify the respective effects of population removal and dispersal strategies. For example, we predict that species with wider dispersal potential should be less sensitive to removal of life history or habitat nodes, but both are dependent on realized spacing and scales of dispersal. For managers and ecologists, this data will represent a significant breakthrough.

EXPERTISE AND CONTRIBUTION OF TEAM MEMBERS:

Snelgrove is a larval ecologist who has published extensively on larval transport in invertebrates and fish. He will be responsible for collection of ichthyoplankton data using ring nets, Tucker trawls and neuston nets, and will oversee laboratory processing of these samples. **Snelgrove** and **deYoung** will co-supervise a *PhD student* project based on the egg data. **deYoung** is a physical oceanographer with extensive experience in physical-biological modelling and in fisheries management issues (as a member of the Fisheries Resource Conservation Council). A Postdoctoral Fellow (part time), supported independently by **deYoung**, will support the field program and aid in developing and interpreting some of the bio-physical modelling. **Gregory** is a behavioural ecologist with particular expertise in fishes, and he will coordinate gap-crossing experiments and demersal juvenile sampling efforts. **Gregory** fills a dual role in this project, first as an adjunct scientist with MUN as an academic colleague but also as a DFO Research Scientist with strong knowledge in juvenile fish ecology who brings significant resources to the project. **Gregory** will supervise Morris, who will collect data for his PhD. **Gregory** and **Snelgrove** will supervise the *MSc student* who will be responsible for juvenile sampling and experimentation. **deYoung** will be responsible for physical data collection and modelling, and will supervise an *MSc student* project that will apply the physical-biological model. **Snelgrove** and **deYoung** will work closely on this process. **DiBacco** is an expert on the use of geochemical tags for larval tracking, and will supervise the full time *postdoc* **Bradbury** who will be jointly responsible for otolith collection and analysis. **Pike** will implement and analyse graph theoretic models, with the aid of an *MSc student* under **Pike**'s supervision. **Pike** is a mathematician whose primary expertise is graph theory and graph models that have utility in network connectivity (e.g. feedback avoidance, Pike 2003; Pike and Zou preprint). **Bentzen** is an expert on population genetics and an authority on cod population structure; he will oversee the genetics work. All members of the team will participate in the development of the connectivity model because it will involve all life history stages. The research team is also well integrated. **Snelgrove** & **deYoung** are frequent collaborators, and **Snelgrove** supervised **Bradbury**'s MSc thesis, on which **deYoung** was a committee member. **Bentzen** is his current PhD co-supervisor. **Gregory** and **Snelgrove** have collaborated on other proposals. **DiBacco** is new to the group but is well known to **Snelgrove** from meetings on larval recruitment. **Pike** further contributes to the interdisciplinary nature of the research and represents a new collaboration.

PROJECT WORK PLAN

The project has 7 distinct components: field collections of eggs/larvae and juveniles, biophysical modeling, lab otolith calibration, otolith chemistry, genetics, and application of Graph Theory.

Year 1: We will collect field data on eggs, larvae and juvenile distribution and movement. In April, **Snelgrove** will oversee high-frequency ring net sampling in Trinity Bay in order to define more clearly the gridded survey that will place in ~ early June. In early June, a field team overseen by **Gregory** (and Morris) will map habitat (GIS) in the five study bays. Experimental work on juvenile fish by **Gregory** will occur August-September; broader scale seining survey will begin in September. Fall seining will be paired with neuston sampling. Ancillary CTD (conductivity, temperature, depth) data will be collected throughout. Egg/larval data from Yr 1 will be integrated into **deYoung**'s existing model to project patches forward and match with observations. A high-resolution (50 m grid scale) model being developed by **deYoung** and co-workers for St. John's Harbour will be applied to Smith Sound. **Gregory** and **Bradbury** will obtain otoliths and tissue for DNA analysis from DFO fall surveys and from juveniles in our seine surveys. **Bentzen** will develop genetic markers. **Snelgrove** will oversee juvenile tank-rearing experiments with input from **Bradbury** and **DiBacco**; undergraduates will be hired to assist with this work through a MUN student employment program. A workshop late in Yr 1 for the team and stakeholders will facilitate exchange of ideas and refine plans for Yr 2, integrating **DiBacco**, **Bentzen** and **Pike**. **Gregory** and **Snelgrove** will lead dissemination of project results to stakeholders and team members, including annual progress reports. Data reports will be prepared on each component of the study for sharing within the team and for documentation of the field work accomplished.

Year 2: Responsibilities and activities will be similar to Yr 1. We will use collected data to refine our sampling protocol. **deYoung** will develop the null model on physical connectivity among bays. **Bradbury** will begin postdoctoral research with **DiBacco** and **Bentzen**, by working at MUN with **Snelgrove**, collecting otoliths and tissue samples for genetics from lab and field collected individuals. In summer, he will relocate to UBC to analyze microchemistry of otoliths from Yr 1 and 2. In addition, **Pike** will begin graph theoretic model development as component data become available.

Year 3: We will complete otolith sample and genetic processing and integration of life history components for development and analysis of graph-theoretic models, where **Pike** will play a key role. The biological and physical data will be analysed and available for the final bio-physical model simulations. We will develop independent and integrated manuscripts for publication on the work done

SECTION 2 – TRAINING PLAN:

Student training is central to this project, and much of the budget is for undergraduate, graduate student and postdoctoral salaries. The *postdoctoral position* (**Bradbury**) will be dedicated to developing and completing the otolith work with **DiBacco** and the genetic work with **Bentzen**; otolith microchemistry is an emerging field with multiple applications in conservation and management, and is particularly powerful in concert with genetics. This postdoc will also help to integrate the MUN, Dal, and UBC components. We envision at least *six graduate students* will be involved in the project, *one PhD* in larval ecology and dispersal with **Snelgrove** and **deYoung**, *one MSc* in juvenile fish habitat use with **Gregory** and **Snelgrove**, and a third in physical oceanography with **deYoung**. A 2nd Post-Doctoral fellow (part time) will be supervised and independently supported by **deYoung**. A fourth *graduate student* will work with **Pike** on the Graph Theory application. Corey Morris, a technician in **Gregory**'s lab, is currently beginning a part-time PhD that will utilize data from this project. His salary is paid through DFO. Sarah Ross, an MSc student with **Gregory**, will also utilize some of the data from Yr 1 for her thesis, and her salary will be covered through **Gregory**'s other projects. We also hope to use this funding to leverage support for *additional graduate students* through Memorial University partial fellowships. We will hire *two undergraduates* to assist in field work in each of the first two years (training in **Snelgrove**'s and **Gregory**'s labs). **Bentzen** will employ at least one summer undergraduate student each year to work on this project but fund them other sources. Each sub-project will involve development of specialized skills ranging from taxonomy to genetics to biophysical modelling.

The project is strongly interdisciplinary in nature and we anticipate interaction between all of the participants of the project. The link between physical oceanography and larval recruitment is known to be of great importance, and members of our team have been actively involved in these sorts of successful collaborative efforts in the past. Of particular note is the merging of marine conservation and management with graph theory, which has only recently been adapted as a tool by terrestrial ecologists but with great success. We believe this approach has strong potential for the management of Canada's marine living resources, and our students and postdocs will be at the forefront of the discipline. The large field component of the project will provide hands-on experience in multiple marine sampling techniques. The utilization of otolith microchemistry and genetics will expose students to the most exciting new techniques to emerge in fisheries research; this tool is likely to be widely used in future by fisheries organizations. All PIs have demonstrated track records with graduate student supervision and thesis committees as evidenced by continued student presence in their labs and joint publication of research in scholarly journals. Specific PI supervisory roles are outlined in the "Expertise" section.

The collaboration with DFO will ensure that several of the graduate students will spend the majority of their research time at DFO St. John's, where they will interact with **Gregory** and other DFO scientists. Gregory will also serve on the supervisory committees of other students involved with project.

We will also organize a mini-symposium to discuss the project and its implications, in part to bring **DiBacco** and **Bentzen** to St. John's to interface with the other members of the team and members of the St. John's research community, including graduate students and postdocs. We will also host a second mini-workshop with an outside expert to provide guidance and ideas for the completion of the project.

SECTION 3 - INTERACTIONS WITH NON-ACADEMIC ORGANISATIONS (KNOWLEDGE AND TECHNOLOGY TRANSFER POTENTIAL)

Our current capacity to manage Canada's living marine resources is constrained by a limited understanding of how populations are structured spatially and how this structuring influences temporal and spatial variability in recruitment. This type of information is critical if we are to manage fisheries more sustainably and design marine conservation strategies that are likely to be effective. For example, at present, the scientific basis for the establishment of marine protected areas is very limited, and whether closed areas will succeed in some key goals depends on these connectivity questions.

The tools we will develop with this project will provide a framework for similar efforts in other areas and for other species. One of the strengths of the proposal is in contrasting different life history strategies, and thereby establishing a null model for future work on different sorts of species.

The strong involvement of DFO in the development and execution will provide a direct link to the very organization that manages commercial species in Canada's oceans and protects marine biodiversity resources. Dissemination of information will be achieved through presentations to DFO (including the Fisheries Oceanography Committee) and also to the broader scientific communities.

In Newfoundland, the remaining biomass of demersal fish species resides inshore following intense offshore fishing. Of these species, more than 60% are listed or are candidates for COSEWIC designation (e.g. Atlantic cod, Greenland cod, shorthorn sculpin). Using available data (i.e., population trends, habitat associations, life-history characteristics), these species are individually assessed to determine if they are eligible for "at risk" status in Canada. Following such a listing, the Canadian Species at Risk Act (SARA) mandates that the critical habitat for that species (i.e., habitat necessary for the survival or recovery) be identified and considered in a recovery strategy. To date, the implementation of recovery plans has been slow and consequently, there has been pressure from conservation groups to streamline the process. This is largely due to difficulty in identifying critical habitat, scales, and quantifying their role in population recoveries; our project can help with this issue.

Researchers at Memorial University of Newfoundland have a long history of interacting with Terra Nova National Park. The researchers on this project will provide the park with copies of all publications and reports produced using data collected in the marine waters adjacent to the park, and all other documents relevant to the park's interests. Our team (e.g., RSG) has a ten year record of work in the

park intertidal waters, and has collaborated with colleagues directly on research questions (e.g., Cote et al. 2002) and has contributed to the park's interpretive program, with seminars. We anticipate those interactions will be maintained or even strengthened through the currently proposed study

From a public outreach and education perspective, our project will benefit from our partnership with Coastal Connections, a company that takes school tour groups to sample marine environments. Coastal Connections will use students (and tour groups) to collect ring net samples (using our protocols) that we will use to document cod egg production in Smith Sound for our biophysical modelling. In exchange for reduced boat fees, we will provide Coastal Connections with sampling equipment and training, and materials for presentations (including data from previous school tours). This approach will offer real hands on experience for K-12 students and the general public.

SECTION 4 - POTENTIAL BENEFITS TO CANADA AND ANTICIPATED SIGNIFICANCE

Canada has the longest coastline (~250,000 km) and largest offshore economic zone (3.7 million km²) in the world. Throughout this vast area are many populations and fish species. Several marine populations are already believed to be at risk of extirpation as a result of human activities. Our ability to develop conservation plans that will aid in the recovery of threatened and overfished populations will depend upon the extent that lifestage components utilize specific habitat locations and our ability to then protect areas that contribute most to recruitment success. Central to this effort is connectivity, which is the linkage among subpopulations; some subpopulations may provide recruits for other subpopulations whereas others may be sinks. Developing the tools needed to evaluate connectivity is therefore critical for Canada, and an important advance in marine ecological research. Understanding connectivity is pivotal for precautionary management and successful implementation of conservation plans.

Connectivity is a key concept in the management of resource species. The degree of connectivity among life-stages and suitable habitats will influence the rapidity with which populations will exploit new areas or reoccupy such areas following localized extirpation events. Even if suitable habitat areas exist, they will remain unoccupied by individuals of a species if no (or low) connectivity exists between the area and the life stage that would otherwise colonize it. Understanding connectivity is pivotal for Canadians undertaking precautionary management and successfully implementing conservation plans.

Management plans for living-marine resources in Canada are established with two fundamental goals: 1. conserve species and populations; and, once assured, 2. maximize harvest levels. Currently, marine species in Canada are managed on the basis of broad populations within geographic units, but this approach requires spatially-explicit population models to be effective. However, such models have proven difficult to construct – especially for marine fishes – because of large reproductive potential and the vastness of oceans. But a greater hurdle is the lack of information on population structure.

In recent decades, fisheries managers have looked to technologies such as genetic and geochemical markers to determine connectivity. Although molecular genetic techniques are useful for identifying distinct populations sustained through strong isolation or complete self-recruitment, they are insensitive where populations intermingle, but in tandem with geochemical signatures (e.g., in otoliths) it is possible to develop comprehensive tools to describing connectivity in populations that form separate ecological or management units at time scales relevant to managers, such as seasonal or annual migrating units. The implementation of marine protected areas (MPAs) is increasingly seen as an effective tool in marine conservation, both in Canada and abroad. The models developed from our proposed work will identify the spatial scales necessary to conserve critical habitat. MPAs are currently created on an ad hoc basis. Although the best available ecological information is certainly used, managers can often only guess at the potential success of protecting any given area because of a paucity of connectivity information. To date, there have been no quantitative means of evaluating one area over another or determining the size of area to be protected. By examining connectivity among life history stages and links to physical habitat, our proposed work will determine the size and locations of habitat necessary to maintain populations. These techniques will also be readily transferable to other populations, species, and regions of Canada and elsewhere.

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