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# Sampling variability of ichthyoplankton surveys—Exploring the roles of scale and resolution on uncertainty

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ABSTRACT

We examine the accuracy of predictions from a conceptual model dealing with survey design in a variable environment using data collected from a number ichthyoplankton collections carried out off Newfoundland, Canada. We test predictions concerning the effects of spatial scale, survey resolution, as well as the impacts which variations in environmental forcing and survey duration have on the precision of population estimates. Although the size of the survey area does not appear to influence the precision of population estimates, the distance between stations, the variability in wind forcing of currents, and the time taken to cover the area of interest all have notable effects on precision. The significance which each of these variables may have on the ability to detect changes in population abundance is likely to vary depending on the underlying circulation that characterizes different ecosystems. Our findings, however, point to the potential benefits that may be derived from evaluating the possible influence of such variables on the precision of population estimates based on long standing monitoring programs. This may serve to explain why it has been so difficult to detect substantial changes in vital rates obtained in process-oriented research.

## 1. Introduction

Ichthyoplankton surveys are essential tools in the study of the early life stages of fish, whether the objective is to gain understanding of the processes that affect recruitment variability or to estimate spawning stock size using egg or larval production methods (Stratoudakis et al., 2006; Houde, 2008). In general, surveys are designed to provide accurate estimates of abundance, and they must be sufficiently precise to either detect changes in vital (i.e., mortality) rates that affect survival (for research into processes regulating recruitment) or to permit the meaningful back-calculation of egg production (for a fishery-independent measure of spawning stock biomass). In practice, however, most surveys are treated as quasi-synoptic and disregard the effects of currents that affect the spatial distribution of ichthyoplankton during the survey. Yet it is well known that ichthyoplankton are distributed in a highly patchy manner.

Any in-depth consideration of how the spatial distribution of ichthyoplankton affects surveys, or, more generally, of how the distribution of plankton depends on the environment, ultimately involves discussion of the relevant physical and biological length and times scales operative in the system. Such scales are myriad and include those describing the physical setting (e.g., shelf or bay width), external forcing (e.g., the frequency of storms), circulation (e.g., the magnitudes of mean and fluctuating currents), vital rates and predation (e.g., mortality), and survey design (e.g., duration). These scales often differ among surveys, either among cohorts or regions, thus confounding the comparison of results. The ratios of these scales, one to another, also determine which physical and biological processes are likely to be important during a survey. For example, the turnover rates of phytoplankton and zooplankton populations relative to their rates of dispersal and loss from grazing and/or predation have strong influences on the spatial scale of patchiness. Mackas et al. (1985) conclude that the approximate proportionality between spatial extent and temporal persistence of physical features in the ocean provides a basis for estimating the relative effectiveness of the biological rates (e.g., competition coefficients, population growth rates, motility, and predation) responsible for patch generation.

The distribution of phytoplankton tends to correspond more closely with the scales of variability of physical tracers (salinity, temperature), with relatively large spatial scales dominating (also referred to as a red spectrum), whereas the patterns observed in zooplankton become more significantly influenced by species interactions, physiology and behaviour as body size increases, which leads to greater patchiness at small spatial scales. Ichthyoplankton distributions are a special case: first, they depend on their initial state which results, in part, from the aggregation scales of spawning adults; second, a cohort is not influenced by

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reproduction. At first, changes in patchiness are determined by physical processes; later, behaviour (Hewitt, 1981) and spatial patterns in mortality (Portilla et al., 2007) become increasingly important. Whereas zooplankton communities may demonstrate an affinity or association with specific water masses, the roles of drift and retention for ichthyoplankton are highly variable and can result in a high degree of dispersal and patchiness that may create important challenges when trying to obtain a representative sample of a population.

Helbig and Pepin (1998a,b; hereinafter referred to as HPa,b) argued that the sampling resolution used in a survey relative to physical and biological scales of variability in the ocean as well as the manner in which a survey is carried out, can significantly affect both the accuracy and the precision of abundance estimates. They introduced a theoretical framework that takes into consideration the structure and variability of currents and eddies, which are critical elements influencing the dispersion of plankton. Their framework provides predictions of the bias and variance of abundance estimates from different survey designs. From application of this framework, they concluded that a sampling plan that fails to adequately resolve the energetic space and time scales of the plankton distribution will generate population estimates (i.e., estimates of mean abundance over the survey area) whose variance is greater than natural levels (HPa) and thereby affect our ability to answer biological questions about the early life history of fish. This means that the sampling scheme must (1) resolve the main physical features that govern the spatial distribution of the organisms of interest, and (2) be carried out in a timely manner so as to avoid significant changes in distribution over the course of the survey.

The HPa model uses a spectral representation of the space–time variability of currents and plankton in which the variance in the system is partitioned in terms of length and time scales. This formalism provides a substantial base for exploring the consequence of different environmental conditions on the ability of alternate survey designs to adequately sample dynamic populations. However, the knowledge requirements of this framework are substantial: space–time spectra of plankton and current fields, particularly over a broad range of environmental conditions, are difficult to obtain. Furthermore, the design of oceanographic surveys is often done in the face of substantive logistical constraints (e.g., vessel availability, ports of call, ability to process samples, etc.). As a result, there has been limited application of the principles outlined by the framework (e.g., Voss and Hinrichsen, 2003; Panteleev et al., 2004; Oozeki et al., 2009).

The key issue in survey design in different or varying environments is the need to be able to interpret the uncertainty in population surveys. Some important predictions (rules-of-thumb) that emerge from HPa are: (1) that it is essential to resolve key oceanographic features that affect the aggregation and dispersal of plankton, otherwise the variance and bias of population estimates will increase; (2) as larger areas are sampled, variability in abundance estimates may increase in instances where the large scale spatial variability dominates that at small scales (red spectrum); (3) as forcing becomes more energetic, horizontal and vertical mixing will increase, thus partially homogenizing patches and thereby potentially reducing variability in abundance estimates; (4) increasing the survey period, particularly in areas with recirculation, may decrease the independence of observations and therefore result in lower uncertainty than is true.

In this study, we will examine the dependence of the precision of abundance estimates on the spatial scale of the region sampled as well as on the spatial sampling resolution using data collected from a number ichthyoplankton collections carried out off Newfoundland, Canada (Fig. 1). We also examine the accuracy of the predictions from the HPa model. Our objective is to understand the factors that can influence our estimates of the variance in population abundance obtained during each survey, by providing an empirical evaluation of the model's general predictions. The analyses presented here are intended as exploratory because the number of surveys (i.e., observations) available is limited and the estimation of variance of population estimates from surveys is a task fraught with numerous sources of error. Our analysis is based on the information collected for several species of fish eggs and larvae during each study, where each species or stage is treated as an independent realization of the pattern of spatial variability characteristic of the study period. These observation-based analyses are augmented with a set of calculations made using the HPa model that serve to explain some of the dependence found on spatial scale.

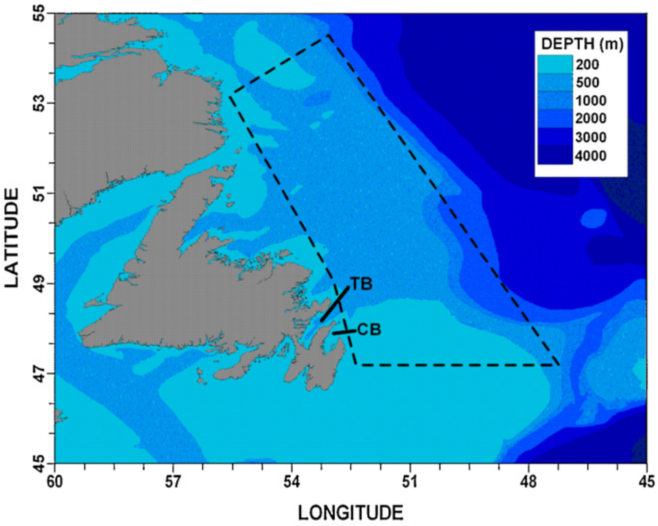

**Fig. 1.** Map showing the areas from which ichthyoplankton data were collected. The two coastal areas are indicated by paired letters at the mouth of each bay (TB – Trinity Bay; CB – Conception Bay). The large polygon represents a rough outline of the area of the Newfoundland Shelf that was sampled during the offshore surveys. Not all the area was sampled during each offshore survey because of logistic constraints caused by vessel capacity, weather and pack ice.

## 2. Methods

We collated the data from 18 ichthyoplankton population studies in which we participated (Table 1). The studies consisted of one study of three distinct patches ($\sim$150 km$^2$) (Pepin et al., 2002), four broad scale surveys of the Newfoundland Shelf (>100,000 km$^2$) (Pepin and Helbig, 1997), two surveys of a large bay – Trinity Bay (3000 km$^2$) (Baumann et al., 2003; unpublished data) and 11 surveys of a smaller bay – Conception Bay (Pepin et al., 1995, 2003; Pepin unpublished data) (1000 km$^2$) (Fig. 1).

Sampling of the continental shelf generally took roughly two weeks, although one survey (HAM230), focussed on a area $\sim$15,000 km$^2$ and lasted only 3 days. The survey design was based on a set of standard oceanographic sections and was aimed at providing a census of ichthyoplankton over what parts of the shelf were open to sampling (i.e., ice-free) during the period of April to June. The cross-shelf station spacing was approximately 20 km while the spacing between transects along the shelf was about 100 km. Station spacing in the cross-shelf direction was chosen to as small as possible subject to available ship time.

Sampling of coastal areas generally occurred over periods of one to two weeks during which time the grid was sampled from one to three times at roughly weekly intervals, which corresponds to the weather band of variation in wind forcing in the area (HPb). Station separation and arrangement varied greatly among studies but was typically chosen to ensure that it was similar or less than the internal Rossby radius *Ri*, at least in the cross-bay direction.