Power of monitoring surveys to detect abundance trends in depleted populations: the effects of density-dependent habitat use, patchiness, and climate change

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Traditionally, trawl surveys were designed to collect fishery-independent data for assessing the population dynamics of commercially exploited species. However, trawl survey data are increasingly used to describe the abundance, distribution and ecology of a wide range of species in studies of climate change and fishing effects. These new uses of survey data suggest that improved understanding of the value and limitations of existing survey designs is required. We compared the power of different survey designs (where stations are fixed, fixed stratified, random, or random stratified) to detect known trends in the abundance of depleted populations. Modelled populations were characterized by different temperature preference, density-dependent habitat selection, and patterns of small-scale aggregation (patchiness). Temperature preferences and local patchiness had an influence on the power of different surveys to detect increases in abundance, and in some scenarios, survey-area indices would consistently underestimate or overestimate trends in overall abundance. As the distributions of many fish populations have shifted in response to climate change, exhibit distribution-abundance relationships, and have been depleted by fishing, we conclude that survey indices may provide partial or unreliable information on changes in the true abundance of the wider range of species now of interest. To disentangle the effects of fishing, climate, and biology on the abundance of fish populations, and to monitor the depletion and recovery of species threatened by fishing, there should be greater emphasis on coordinating the timing, areas of coverage, and methods of sampling of surveys of the Northeast Atlantic continental shelf.

Keywords: climate change, density-dependent habitat use, ecosystem approach to fisheries, fish population, monitoring, survey design, trawl survey.

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Introduction

Most trawl surveys were established to provide fishery-independent abundance, distribution, growth, and maturity data for target populations. Although surveys were often intended to cover the range of these populations, their design was inevitably a compromise, the distribution of some populations being centred in the survey area, and those of others centred on the margins or outside the area. In recent years, trawl surveys have also been used to describe the abundance and ecology of non-target species and fish communities, along with changes in fish distribution with climate change, consistent with a growing interest in the wider state of the marine environment (Greenstreet and Hall, 1996; Beare *et al.*, 2004; Blanchard *et al.*, 2005a; Perry *et al.*, 2005). Generally, however, the surveys were not designed to provide data to support such analyses.

Both statistical and practical considerations have influenced survey design. As well as trying to cover the spatial range of target populations with a statistically rigorous approach, ship time may be limited, all areas may not be fishable with trawls, and a high risk of gear loss or damage may be unacceptable.

Surveys are often stratified or post-stratified (Smith, 1997; Sparholt and Tomkiewicz, 2000; Dressel and Norcross, 2005). Stratification improves the precision of abundance estimates when the variation among samples (tows) within each stratum is less than the variation among tows in the whole survey area (Hilborn and Walters, 1992). With a stratified survey, separate abundance estimates are produced for each stratum and used to calculate an overall weighted mean abundance, where weights for each stratum are proportional to stratum size. Within strata, sampling can be systematic or random. Systematic sampling introduces bias if trawl tows are aligned with an environmental gradient, but systematic grids minimize this possibility. As there are gradients in fish density, systematic sampling provides more precise abundance estimates than random sampling (Hilborn and Walters, 1992). Moreover, systematic grids make good use of ship time, ensure that tows avoid major physical obstructions, and usually minimize the risk of missing density concentrations. On the other hand, it is easier to calculate survey precision with a random design, and easier to adapt a random survey when time is lost through bad weather, and a potential problem with

fixed station designs is the bias introduced if some stations are missed in certain years (ICES, 1992).

Recent changes in fish populations and the use of survey data suggest that survey design needs to be re-examined. First, many fish populations have been depleted by fishing since surveys were established and are now caught infrequently in a small proportion of their former range (Brander, 1981; Quero, 1998; Walker and Hislop, 1998). Second, the distribution of many populations is shifting with climate change, and changes in abundance will be confounded by changes in distribution (Beare *et al.*, 2004; Perry *et al.*, 2005). Third, surveys may be used to assess the decline and the recovery of many rare and vulnerable non-target species that are a focus of conservation legislation, and the survey area may not cover their entire range (Dulvy *et al.*, 2004; Maxwell and Jennings, 2005).

Many fish populations show density-dependent habitat selection (DDHS), their ranges contracting as abundance falls. At very low abundance, fish populations may be confined to small areas of optimal habitat (Myers and Stokes, 1989; Marshall and Frank, 1995). This makes them highly vulnerable to targeted commercial fishing effort, but reduces the probability that abundance will be adequately estimated by surveys when stations are widely spaced (Hutchings, 1996). At greater levels of abundance, DDHS also means that populations not centred on the survey area may expand and contract out of the area as abundance changes. Therefore, changes in local density may not reflect changes in true population abundance.

To assess the effects of DDHS on survey design, distributionabundance relationships need to be predicted. Ideal free distribution (IFD) theory provides a simple approach for predicting relationships between distribution and abundance (Fretwell and Lucas, 1970). It assumes that all individuals have the same competitive ability and are free to move to areas that maximize their fitness. Because, underlying habitat suitability is positively related to fitness, and increased density reduces fitness, individuals spread into less preferred habitats as local density increases. When population size is low, the model predicts that individuals only occupy areas with the very highest habitat suitability. As population size increases, individuals spread into less favourable habitat and, when the total population size equals the carrying capacity, all habitats are occupied (McCall, 1990). According to IFD theory, individuals spread until they achieve equal fitness. Fitness is not easy to measure at large scales in the marine environment, but growth rate is one measure of fitness and can be linked to temperature and prey availability (e.g. Hughes and Grand, 2000). Blanchard et al. (2005b) showed that temperature can be used as a surrogate for habitat suitability at large spatial scales, a useful finding when the data needed to directly measure the multiple components of true habitat suitability (e.g. prey density, substratum, predation risk) are not available at appropriate scales.

The interaction between DDHS and changes in habitat suitability because of climate variation and change may further confound the capacity of surveys to detect changes in population abundance. Moreover, with some heavily fished populations depleted to 70–90% of their former adult abundance and/or theoretical carrying capacity (Hutchings and Baum, 2005), surveys have to detect changes in the abundance of fish that may be found in a tiny proportion of their former range. Unfortunately, the requirement for accurate abundance estimates probably increases with decreasing abundance, because depleted populations are the focus of recovery plans and have truncated age structures that make them more vulnerable to excessive

fishing mortality and environmental variation (Trippel et al., 1997; Berkeley et al., 2004).

The aim of this study is to assess the power of different survey designs to detect known (true) trends in the abundance of depleted populations, recognizing that the range of populations will often cross the boundaries of survey areas. Modelled populations were characterized by different temperature preferences and patterns of small-scale aggregation (patchiness). All modelled populations exhibited DDHS. The abundance and temperature preferences of the modelled populations were used to determine their overall distribution, and survey abundance indices were calculated from catches in the area currently sampled by the North Sea International Bottom Trawl Survey (IBTS).

Methods

The approach used combined models that accounted for several biological processes, statistical sampling procedures, and power analysis. Figure 1 shows the basic approach and the steps required for the analysis.

Step 1. A model of distribution—abundance relationships, based on IFD theory, was used to predict how the local abundance of a population, at the scale of an International Council for the Exploration of the Sea (ICES) statistical rectangle (area of rectangle 3720 km² at 53°N), in the North Sea, would change with total (true) population abundance in Northeast Atlantic seas that surround the British Isles (area bounded by 48.5–63.75°N, and 11.5°W–11.5°E; Figure 2). Changes in true abundance were described for population sizes much lower than the theoretical carrying capacity and for populations with distributions centred in the southern, central, and northern North Sea.

Step 2. The spatial distribution of individuals within ICES rectangles was modified to account for different levels of patchiness

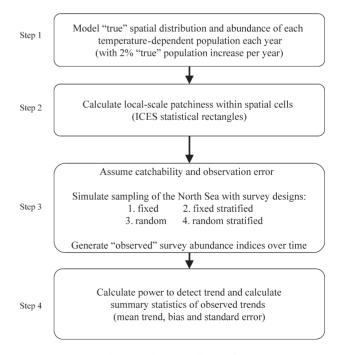


Figure 1. Steps used to simulate the effects of temperature-dependent distribution and abundance, patchiness and survey design on the power to detect recovery of depleted populations.

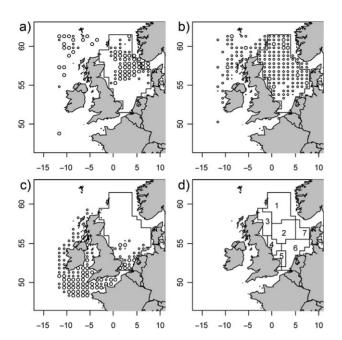


Figure 2. Map showing the predicted distribution and abundance of the theoretical populations at 1% of their carrying capacity (K), and for temperature optima of (a) 5.4°C, (b) 8°C, and (c) 13.5°C. Abundance is proportional to the area of the circles, expressed in relation to the maximum population size reached across simulations (10^7 individuals). The boundaries of the North Sea survey area are superimposed on all panels, and (d) shows the seven strata within the area.

within rectangles (e.g. shoaling behaviour and local habitat association).

Step 3. These resulting patchy distributions were "sampled" based on an assumed sampling effort (tow length), catchability, and observation error, then indices of abundance were calculated from the simulated catches, for four different survey designs.

Step 4. For each of these designs, trends in "observed" survey abundance indices were compared with trends in true abundance, and the power of the survey to detect trends in abundance was assessed.

Distribution - abundance model

The abundance of individuals in ICES rectangles was predicted using an IFD model, where the observed mean annual bottom temperature in each rectangle was used as a proxy for habitat suitability. Distribution—abundance relationships were modelled, based on IFD theory, following McCall (1990), where the additional negative effect of density dependence on habitat suitability was incorporated as:

$$r_i = B_i(1 - kN_i), \tag{1}$$

where r_i is the realized suitability in rectangle i, B_i the basic temperature-dependent habitat suitability in rectangle i, N_i the local adult abundance, and k is the density-dependent coefficient, reflecting the rate at which individuals spread into less-preferred habitats as local abundance increases. The total population size N must equal the sum of all N_i from i = 1 to n, where n is the total number of locations. IFD is an evolutionary stable strategy, and therefore assumes that, at equilibrium, only the habitats that allow individuals to achieve maximum and equal fitness (r^*) are

occupied. To determine the equilibrium (r^*) across all habitats, the model is run iteratively (t=1, 2 ..., n), where n is reached when $\partial r/\partial t = 0$. According to Equation (1), the maximum population size (carrying capacity of the habitat) is inversely related to the k parameter (K=1/k), where K is defined as the total population size at which $r^*=0$ and all habitats are occupied (McCall, 1990).

The definition of habitat suitability followed Blanchard *et al.* (2005b), habitat suitability being determined by temperature. The study area was divided into grid cells corresponding to ICES rectangles (0.5° latitude by 1.0° longitude), and the temperature in each grid cell was defined as the annual mean bottom temperature averaged over the period 1992–2002. These data were obtained from ICES. In the absence of other examples, we used the relationship between temperature and growth rate for cod from Björnsson and Steinarsson (2002) to describe the form of the relationship between habitat suitability and fitness. We set the optimal temperature at 5.4, 8, and 13.5°C in our scenarios, corresponding to distributions covering the mid-northern, central, and mid-southern North Sea.

Trends in true abundance

We considered changes in true abundance for populations that had been reduced to 1% of their theoretical carrying capacity (K), where K was assumed to be 10^{10} . This level of population reduction is consistent with reductions observed in some target and non-target populations (Hutchings and Baum, 2005). A reduction of 99% is also consistent with the predicted declines in abundance of the largest fish in the North Sea (Jennings and Blanchard, 2004). We considered the power of the survey to detect a 2% year-on-year recovery in adult abundance from a starting population that was 1% of K. This proportional rate of increase is slower than the expected intrinsic rates of increase for vulnerable species at low population size (Maxwell and Jennings, 2005), but is an approximation of the rates of increase that might be realized over several years in the presence of continued fishing mortality.

Patchiness

The patchiness of the spatial distribution of fish within each rectangle was described using the negative binomial probability distribution, which is commonly used to model overdispersed count data (McCullagh and Nelder, 1989). For a random variable *Y* that follows a negative binomial distribution, the mean, variance, and probability function are defined as

$$E(Y) = \mu, \quad \text{var}(Y) = \mu + \frac{\mu^2}{\theta},$$

$$f_Y(y; \theta, \mu) = \frac{\Gamma(\theta + y)}{\Gamma(\theta) y!} \frac{\mu^y \theta^\theta}{(\mu + \theta)^{\theta + y}}$$
(2)

(notation matching Venables and Ripley, 2002, p. 206). The variance: mean ratio ($\varphi=1+\mu/\theta$) was used to describe local-scale patchiness of the distributed fish, following O'Brien *et al.* (2000). The three levels of patchiness we used were based on the values obtained in a sub-rectangle-scale study of variation in survey catches (Ehrich *et al.*, 1998). Average variance: mean values for haddock, *Melanogrammus aeglefinus* (15), whiting, *Merlangius merlangus* (75), and herring, *Clupea harengus* (219), allowed us to represent a broad range of patchiness levels that should capture realistic among-species variation. The level of

patchiness can also vary within species as a consequence of behavioural, life stage, or habitat effects. The range of variance: mean ratios within species demonstrate this and were 0.6–45 for haddock, 1.7–337 for whiting, and 0.4–898 for herring (Ehrich *et al.*, 1998).

Survey designs and abundance estimates

Four survey designs were considered: (i) fixed, (ii) fixed stratified, (iii) random, and (iv) random stratified. The first design, fixed, was based on the existing design of the English North Sea Groundfish Survey (EGFS), during which alternate rows of ICES rectangles running East—West are sampled. Data collected on the EGFS contribute to the IBTS for the North Sea. The requirement for the EGFS to cover the whole North Sea and to contribute to the IBTS has influenced survey design.

Of the 75 stations that should be sampled annually on the EGFS, prime stations 3, 13, 30, 40, 50, 52, and 71 were dropped from the analyses to standardize n in all the designs we considered (n = 68). These stations were dropped because they were outside the main North Sea (71) or were inshore and/or very close to other stations. The second survey design, fixed stratified, was based on dividing the North Sea into seven strata based on the North Sea Roundfish Areas or RFAs (ICES, 1999). These strata, shown in Figure 2d, were selected because they correspond to distinctive bathymetric areas, fish and invertebrate communities, and different levels of fishing effort (Callaway et al., 2002; Daan et al., 2005). Stations within strata were selected on a systematic grid and the values of n within the seven strata were: 22(1), 15(2), 7(3), 4(4), 4(5), 12(6), and 4(7), reflecting the area and habitat diversity of each strata. The third design, random, involved randomly selecting 68 rectangles in each simulation from the 132 ICES rectangles in the North Sea survey area, and placing one station in each rectangle selected. For the fourth design, random stratified, the North Sea was also divided into the RFA strata. Survey stations (one per rectangle) were selected randomly within strata in each simulation, with the same n in each stratum as for the fixed stratified design.

The abundance of fish "caught" using each of the survey designs was calculated by assuming a fixed trawl efficiency of 0.5 and a lognormal observation error with a coefficient of variation of 0.1 (Pastoors *et al.*, 2007). Each survey abundance index was expressed as a mean over selected rectangles or a weighted mean by stratum.

Power analysis

Statistical power is defined as the probability of a specified test detecting a statistically significant result. We used simulation to estimate the power of linear regression with a Type 1 error rate α of 0.05 to detect a trend in log (survey index). This was suitable, because the underlying modelled population had an annual percentage increase in abundance, and relevant, because analysis of survey trends is common for species not considered by stock assessments. Simulated survey indices were generated based on the rectangles surveyed, their population abundance from the IFD model, and within-rectangle variation in catch from the local patchiness. Power was then calculated as the proportion of times, out of the total number of simulations, that a statistically significant relationship was detected in the survey index across years. One thousand simulations were carried out for all survey designs. Rectangles were selected randomly within each simulation for the random designs. The mean power from the 1000 simulations was then used to compare the survey designs. Power was presented as the probability of detecting a trend with between 3 and 30 years of monitoring, for each survey design, for each temperature optimum, with and without temperature change. As trends in survey and true abundance are not necessarily proportional, especially when much of the population lies outside the survey area, we also calculated the bias and the precision (standard error of mean) of the estimated trends to derive the goodness-of-fit (root mean squared error, rmse) between the "true" population trend and the "observed" survey trends obtained from 3 to 30 years of monitoring.

Climate change

The combined effects of climate change and changes in "true" population size on survey abundance indices were assessed by assuming that the temperature in all rectangles was increasing by +0.026°C per year as the population size changed. The rate of temperature increase was based on the IPCC (HadCM3A1F) future climate change scenario (Clark *et al.*, 2003). We made the simplifying assumption that the thermal preference of populations would not change over time, and that populations were free to redistribute themselves in response to temperature. In reality, the local ecology encountered by the shifting population is expected to influence abundance and the extent of redistribution.

Results

The distributions of the modelled populations in relation to the survey area were determined by temperature preferences and distribution—abundance relationships (Figure 2). The extent to which the populations overlapped the survey area and/or the range of the populations changed in response to climate change, and determined the proportion of individuals found in the survey area. Variability in abundance among survey stations was further modified by local patchiness in abundance.

As the abundance of the modelled populations increased, the number of years of survey monitoring required to detect increases in abundance with a power of 0.9 depended on the proportion of the population outside the survey area (dictated by temperature preference of the population), the level of local-scale patchiness, and the survey design used (Figure 3). We tested the relative effect of each of these factors on power over time by including power as the response variable, with the number of years monitoring as the first predictor variable, followed by each factor as a single interaction term in a logistic generalized linear model. The lowest model Akaike Information Criterion and residual deviance resulted from including patchiness as a term, followed by optimal temperature, then survey design. These accounted for 85, 69, and 69% of the variation across the entire model output, respectively.

Power was highest for all survey designs when $T_{\rm opt}=8^{\circ}{\rm C}$ (population distributed predominantly in the North Sea) with low levels of patchiness (Figure 3). Power was lowest for all survey designs for warm-water ($T_{\rm opt}=13.5^{\circ}{\rm C}$), patchy populations without climate change. However, with climate change the effect was reversed, and surveys detected a trend for colder water populations ($T_{\rm opt}=5.4^{\circ}{\rm C}$) less reliably. In all cases the fixed stratified design performed best, although the number of years of monitoring required to reach a power of 0.9 varied from 10 to 25 years without climate change, and depended on the temperature preference and level of patchiness of the population (Figure 3). With

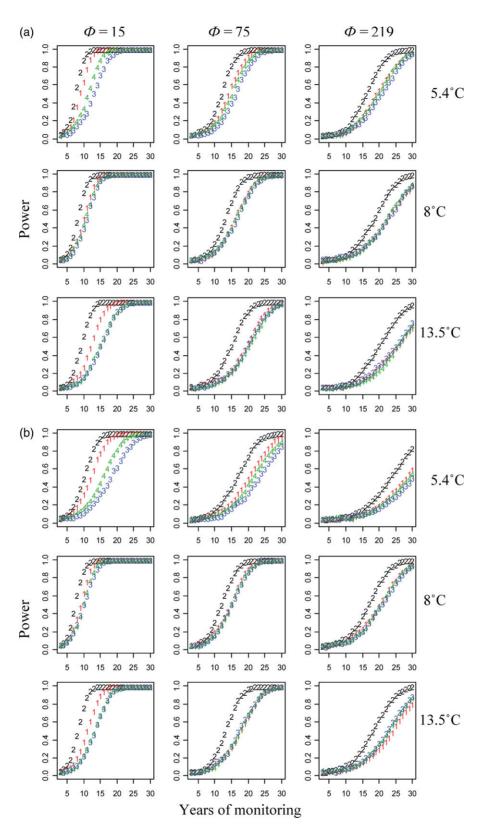


Figure 3. Power to detect temporal trends in abundance for northerly, patchy species (a) without temperature change, and (b) with temperature change for different survey designs (1, fixed; 2, fixed stratified; 3, random; 4, random stratified). The points plotted for random designs (3 and 4) are mean values based on 100 survey-design simulations.

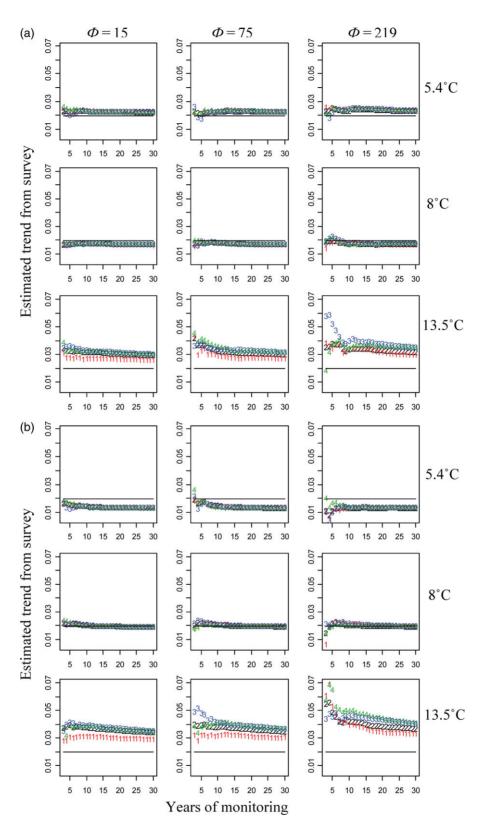


Figure 4. Estimated abundance trends of observed populations obtained from 3–30 years of monitoring northerly, patchy populations (a) without temperature change, and (b) with temperature change for different survey designs (1, fixed; 2, fixed stratified; 3, random; 4, random stratified). The solid horizontal black line shows the "true" trend of the population.

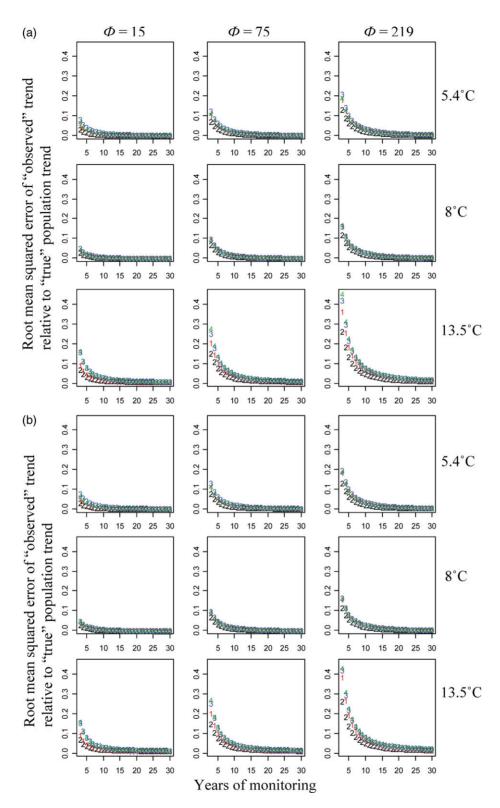


Figure 5. Root mean squared error of the observed population trends relative to the "true" trend obtained from 3–30 years of monitoring northerly, patchy species (a) without temperature change, and (b) with temperature change for different survey designs (1, fixed; 2, fixed stratified; 3, random; 4, random stratified).

climate change, it could take >30 years of monitoring with a fixed stratified design to detect a trend for cold-water ($T_{\rm opt} = 5.4 ^{\circ} \rm C$), patchy populations (Figure 3b).

The degree to which "observed" trends in the North Sea survey indices were consistent with trends in "true" population abundance depended mainly on the optimal temperature preference,

and to a lesser extent on the level of local patchiness and survey design (Figures 4 and 5). In all scenarios the overall population increase was 2% per year, whereas in the North Sea the annual population increase for each temperature preference ($T_{\rm opt}$) was 2.3% (5.4°C), 1.8% (8°C), and 3% (13.5°C) without climate change, and 1.4% (5.4°C), 2% (8°C), and 3.5% (13.5°C) with climate change. The trend estimates from the survey indices were relatively unbiased compared with the North Sea trend, and therefore biased compared with the "true" population trend. This pattern was similar for all survey designs except for the warmer water ($T_{\rm opt}$ =13.5°C) populations where the survey indices produced trends that were overestimates compared with both the North Sea and population trends (Figure 4).

The root mean squared error (rmse) of the trend estimates relative to the overall population increase (Figure 5) or the North Sea average trends (not shown) showed the fixed stratified design to have the lowest rmse. This was due to slightly better precision. In general, goodness-of-fit (rmse) improved with increased monitoring time, and was poor for the patchy warm-water populations.

Discussion

Distribution shifts in response to temperature change, the existence of distribution-abundance relationships, low population size, and the patchiness of local distributions all affect (i) the power of the survey to detect true abundance trends, and (ii) the relationships between survey indices and true abundance. Given that many populations have been depleted by unsustainable rates of fishing mortality (Brander, 1981; Walker and Hislop, 1998), and that the distribution of many populations and species has shifted in response to changing sea temperature (Beare et al., 2004; Perry et al., 2005), our results suggest that it is necessary to consider whether existing survey designs can provide the data needed to support analyses that do not focus on target populations with distributions corresponding to the survey area. This is important when survey data often provide the only available source of information on the decline and recovery of rare and vulnerable non-target species, and on the large-scale biological effects of climate change and fishing in offshore waters.

For fish with an even local distribution, the power to detect increases in abundance from low population sizes after 15 years was relatively high for the survey designs, particularly when the population range was the central North Sea. This was because the survey encompassed most of the populations' range and its use was broadly consistent with its use when assessing the population dynamics of commercially exploited species. Of all survey designs considered, a fixed stratified design had the greatest power to detect a trend, because of its greater precision, although the fixed design had the least bias. Power was much lower for populations with temperature preferences at the margins of the survey area that had moderate to high levels of local-scale patchiness. This was especially true for the warmer water populations, because these did not spread so rapidly into the survey area for a given increase in abundance. Power to detect trends in the populations with a preference for warmer water increased when they also spread north as a consequence of simulated climate change. The converse was true for colder water populations. The degree of local-scale patchiness had the largest effect on statistical power, with power to detect a trend remaining low even after 20 years of monitoring for moderately and very patchy populations.

Stratification improved power when a fixed or systematic grid was used, but only marginally improved power if selection of sampling stations was randomized. According to our results, for populations distributed at the margins of the survey area, with low to moderate levels of patchiness typical of widespread demersal populations, a trend could be detected $\sim 3-5$ years earlier with a fixed stratified design than with the other designs. As the North Sea is a relatively homogenous area compared with other systems, it could be argued that most of the habitat variability would be captured by reducing the number of strata to three depth strata of 0-50, 50-100, and >100 m. Unpublished simulations with these three strata resulted in the stratified designs performing much like the non-stratified designs, with very little difference in power. More finely resolved strata could also be considered, but not without increasing the total number of sampling stations each year.

At the scale of the survey, there have been numerous studies of the effects of survey design on the relationship between survey indices and abundance (reviewed by Kimura and Somerton, 2006). This relationship is influenced by methodological issues such as differences between vessels (Cooper et al., 2004), tow length (Kingsley et al., 2002), and the approaches used to calculate indices (Smith, 1990), as well as in biological issues such as the movements of fish within the survey area during the survey period (McAllister, 1998) and the reliability of species identification (Daan, 2001). However, there has been less emphasis on the effects of multiple processes on abundance indices. When changes in climate and abundance occur simultaneously, as would be expected in most real-world situations, abundance indices can reflect the immigration or emigration of individuals in response to climate, confounded by changes in distribution associated with changes in population abundance. When the survey only covers part of the range of a population, it is effectively impossible to decouple these effects, because the responses of a population to climate change and the distribution-abundance relationship are rarely known. The index/abundance relationships and ability to detect trends are also affected by the number of sites sampled. Sea-based surveys generally have far fewer sites than terrestrial surveys with similar aims. For example, for the UK bird breeding survey, >2000 sites are surveyed annually (BTO, 2006). Cost is a major constraint to increasing replication at sea, but reduced tow lengths (Wieland and Storr-Paulsen, 2006) and survey coordination at a wider scale can be used to increase the number of sites sampled in the same way. However, in practice, tows on most surveys including the North Sea IBTS are already short, with shooting and recovery accounting for much of the total sampling time, and short tows can lead to undersampling of species and individuals that can swim powerfully for sustained periods.

Distribution—abundance relationships are widely observed in fish populations (Swain and Wade, 1993; Swain and Sinclair, 1994; Hutchings, 1996), including those in the North Sea (Blanchard *et al.*, 2005b). Temperature affects on the distribution of species have also been observed (Beare *et al.*, 2004; Perry *et al.*, 2005). As such, modelling the effects of both processes makes a necessary contribution to the assessment of survey design. The modelling of small-scale distributions is more complex and may reflect small-scale habitat variability, local prey availability, predation risk, and behaviour. We could not model these processes explicitly, but used data from a study of small-scale variation in survey catches (Ehrich *et al.*, 1998) to describe patchiness directly.

We assumed that patchiness would not change with total population abundance, but have no data to test whether this is a reasonable assumption.

The results suggest that when most of a population is centred on the survey area (with even to moderate levels of patchiness), the statistical power to detect trends in abundance was fairly good. In reality, however, few populations are effectively covered by surveys such as the North Sea IBTS. Our results suggest that a single survey which covers only part of the range of many of the populations that have become a focus of community studies, and are important when describing the effects of climate change, will not provide the information on distribution and abundance that is necessary to understand the contribution of fishing, climate, and biology to the abundance of fish populations, and to monitor the depletion and recovery of species. We suggest that there should be a greater emphasis on coordinating the timing, areas of coverage, and methods of sampling used by surveys on the Northeast Atlantic continental shelf. Moreover, trawl surveys are unlikely to be appropriate for monitoring populations with very patchy distributions, as has long been recognized (Hilborn and Walters 1992).

Within the Northeast Atlantic, improved information on changes in distribution, and to some extent abundance, could be obtained by linking presence—absence data from existing surveys in contiguous areas. The collection and collation of relative catchability estimates from gear comparison trials can also help, because this would allow standardized catch rates to be estimated. However, these will still be suboptimal solutions when different gears are used for sampling on different types of habitat at different times of year. Our results suggest that if we are serious about understanding the effects of fishing and climate change, and about monitoring the status of severely depleted populations, then it is necessary to try to coordinate the timing and types of survey in the Northeast Atlantic on much larger scales.

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