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# Spatio-temporal dynamics of species richness in coastal fish communities

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Determining patterns of change in species richness and the processes underlying the dynamics of biodiversity are of key interest within the field of ecology, but few studies have investigated the dynamics of vertebrate communities at a decadal temporal scale. Here, we report findings on the spatio-temporal variability in the richness and composition of fish communities along the Norwegian Skagerrak coast having been surveyed for more than half a century. Using statistical models incorporating non-detection and associated sampling variance, we estimate local species richness and changes in species composition allowing us to compute temporal variability in species richness. We tested whether temporal variation could be related to distance to the open sea and to local levels of pollution. Clear differences in mean species richness and temporal variability are observed between fjords that were and were not exposed to the effects of pollution. Altogether this indicates that the fjord is an appropriate scale for studying changes in coastal fish communities in space and time. The year-to-year rates of local extinction and turnover were found to be smaller than spatial differences in community composition. At the regional level, exposure to the open sea plays a homogenizing role, possibly due to coastal currents and advection.

**Keywords:** species richness; time-series; spatial pattern; local extinction; turnover; Skagerrak

## 1. INTRODUCTION

Ever since the nineteenth century, ecologists have tried to understand the spatial and temporal patterns of richness in plant and animal species. In trying to understand richness variation, ecologists have grappled with the spatial scale at which diversity is measured and compared (Brown 1988). A set of terms has been defined to classify this scale: '$\alpha$ diversity' for diversity within a local site or ecological community; '$\beta$ diversity' for spatial turnover in species composition between sites; and '$\gamma$ diversity' for differences in biotic composition between widely separated sites (Magurran 1988). However, it has proven difficult to overcome the problems inherent in dividing an apparently continuous range of spatial variation into discrete units (Brown 1988). Independently of the terms and indices used, the species richness of a site is a result of turnover processes such as (local) extinction, speciation (on the evolutionary time-scale) and colonization. Estimating these turnover rates is of key interest within basic ecology as well as conservation biology (Wilson 1988; Ehrlich & Daily 1993; Pimm *et al.* 1995; Rosenzweig 1995) and may contribute to understanding the scales of biodiversity processes. Such studies clearly require long-term time-series data, that only rarely are available. Using survey data of marine fish communities spanning 45 years and 48 fixed localities, we report in this paper on estimates of rates of local extinction and turnover. Local extinction here describes the situation in which a certain species present at one a point in time (or space) is not present in the next.

A 'zero' observation in sampling data may mean that a species is not present. However, it is also possible that our sampling techniques did not detect the species in question. Many methods for spatial sampling and spatial analyses exist (e.g. geostatistics, Cressie 1993; inventory indices, Clarke & Warwick 1999; rarefaction-related methods, Colwell & Coddington 1994). In this study, we have chosen a method of estimating species richness (see § 4a) that takes both sampling variability and non-detectability into consideration, thus providing stable and reliable estimates of species richness and turnover rates.

Marine communities are characterized by profound stochastic variability (Hjort 1914; Stenseth *et al.* 1999), often rendering multivariate analyses of species-abundance patterns highly unsuccessful when processed without any aggregation of data (e.g. by indices, by averaging across space and time or by studying aggregate entities such as species richness). Hence, ordination methods (e.g. canonical correspondence analysis; Ter Braak 1995) and curve-fitting techniques (Magurran 1988) are not applicable to the data used in this analysis. Furthermore, natural barriers are less influential for spatial distribution of species in the marine biota (Gee & Warwick 1996). Thus, species are not detected with high probability at any single sampling occasion (e.g. Simberloff & Boecklen 1991; Magnuson *et al.* 1994; Greenstreet & Hall 1996; Morrison 1996) and detection probabilities may vary across both

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time and space. However, appropriate methods do exist for estimating species richness from repeated sampling of the same community (Burnham & Overton 1979; Bunge & Fitzpatrick 1993; Colwell & Coddington 1994; Nichols & Conroy 1996) as well as parameters describing community dynamics (Nichols *et al.* 1998*a*,*b*) from repeated sampling of the same community. Applying such methods to long-term and highly standardized survey data provides a means of reducing the variance in the data and at the same time takes sampling variability into account, thereby providing insight into community dynamics parameters (e.g. local rates of turnover and extinction) and the emergent spatial structure (Brown 1995).

Here, we take a fjord-based approach to analyse spatio-temporal patterns of change in species richness and community composition over a 45 year period utilizing a large-scale survey of fish communities along the Norwegian Skagerrak coast taking non-detection and associated sampling variance into consideration. We investigate the spatial and temporal patterns and scale of variation and test for local effects of pollution and regional effects of exposure on community processes.

Our objectives are twofold. First, we evaluate observed patterns in fish communities for the Norwegian Skagerrak coastal system by incorporating non-detectability and sampling variance, thereby implicitly testing if the fjord is an appropriate unit for studying changes in fish communities and supplying estimates of fish community dynamics. Second, we test hypotheses from previously assumed patterns that have not yet been demonstrated, thus contributing to the study of community dynamics of fish communities in the coastal zone. In the following we provide, for the first time to our knowledge for marine communities, estimates of community dynamics parameters explicitly taking sampling variability into consideration, thereby increasing the understanding of ecological processes in the coastal zone.

## 2. THE DATA

Since 1919 more than 250 stations between Kristiansand and the Norwegian–Swedish border have regularly been sampled during September–October by beach seine hauls, with about 100 still being sampled (figure 1). This sampling has followed the same protocol and used equivalent (and highly standardized) equipment throughout the entire survey period. The seines have been replaced several times but all have been constructed according to the same prototype. The leader of the operation has always been the one counting and classifying the species and since 1919 there have been only two leaders (see Stenseth *et al.* 1999).

Each station is given a degree of exposure (i.e. to the open sea) ranging from 1 (low exposure) to 5 (high exposure) based on a subjective assessment of, for instance, the wind, currents and hydrographic conditions (table 1). The Flødevigen monitoring data include a total of 59 species and groups of species. Only fish species are included, leaving a total of 34 fish species as input for the estimation of community dynamics (Lekve *et al.* 1999). Some of the fish species use the coastal zone as a nursery area (e.g. the gadoids, such as cod (*Gadus morhua*) and whiting (*Merlangius merlangus*)), a few species are migratory and use the coastal zone as a feeding ground (e.g. sea trout (*Salmo trutta*) and mackerel (*Scomber scombrus*)) while most species spend their entire lives in the coastal zone (see Lekve *et al.* (1999) for a complete list of species). From release–recapture studies it is known that the cod is highly stationary on a scale smaller than the fjord (Julliard *et al.* 2001), and this is also the experience for most other species (Aa. Sollie, personal communication).

As our purpose here is to estimate the species-richness and community-ecology parameters, multiple sampling within each fjord is required. Preliminary investigations (T. Boulinier, J. D. Nichols, J. E. Hines and N. C. Stenseth, unpublished data; consistent estimates could be obtained for four randomly chosen stations within a fjord) indicate that a minimum of four stations within each area (fjord) should be used as spatial replicates to estimate species-richness and community-ecology parameters. Stations within a fjord were thus viewed as sampling the fish community of a given location; among the time-series available after World War II, 12 areas (or fjords) along the Norwegian Skagerrak coast contained a minimum of four local sampling replicates (table 1) from 1953 to 1996.

## 3. EXPECTATIONS

Spatial patterns of community dynamics may emerge from two sources operating at two different spatial scales:

(i) On a *local* scale, variable dynamics may be seen as a result of environmental and recruitment-related stochastic processes (Hjort 1914; Cushing 1990). Furthermore, the peculiarities of the different localities (e.g. pollution, bathymetry and freshwater run-off) may lead to divergent structures among communities.
(ii) On a *regional* scale we expect the currents in the open Skagerrak Sea to play a homogenizing role by, for instance, advective transport of individuals from some coastal seawater species pool (Johannessen & Tveite 1989; Roughgarden *et al.* 1994; Johannessen *et al.* 1995; Lekve *et al.* 2002), creating a gradient along the coast.

Several studies on dynamics of species richness and composition have in the past focused on the relative role of *local* and *regional* processes in determining the dynamics of extinction and colonization (e.g. Sousa 1979; Ricklefs 1987; Cornell & Lawton 1992; Ricklefs & Schluter 1993; Karlson & Cornell 1998). An emerging new synthesis is that the dynamics of communities ought to be seen within a 'hierarchical patch dynamics framework' (Wu & Loucks 1995) where both environmental stochasticity and biotic feedback interactions may determine the local species richness and composition. In this paper, we adopt such a view by explicitly investigating the community dynamics at ecologically defined levels and specifically combining the local fjord level with the regional coastal level.

Specifically we test previously suggested patterns that communities affected by pollution are less diverse than unaffected communities (Ruud 1968; Johannessen & Dahl 1996; Lekve *et al.* 1999). We furthermore test whether changes in the species richness and composition of com-

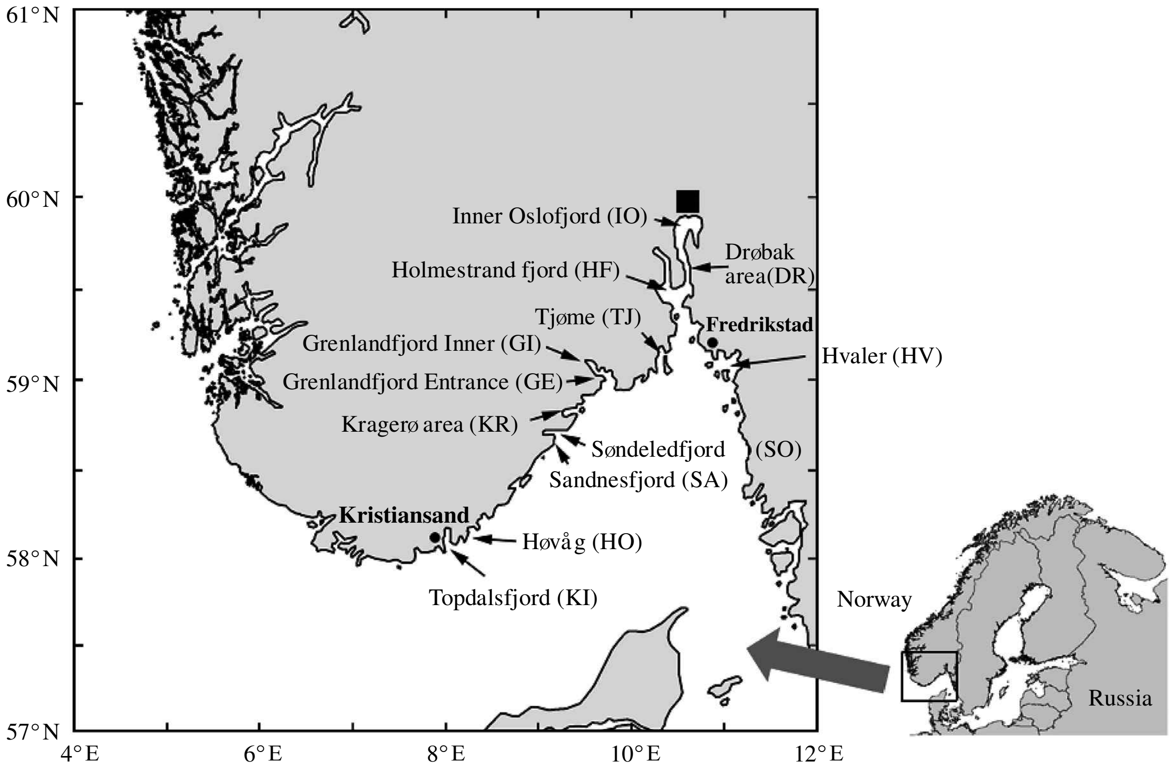

Figure 1. General location of the study areas along the Norwegian Skagerrak coast (lower right-hand corner). Coastline showing the 12 fjords or areas of this analysis, each containing at least four stations that constitute the basis for estimating the number of species and dynamical community parameters.

Table 1. Study areas and sampling stations used as replicates for the fish communities from southwest to northeast. (The general geographical properties of the fjords are characterized according to, for example, length and width of the fjord, depth, presence of a sill, etc. (see Fromentin *et al.* (1997) for details).)

| name of the area | abbreviation | sampling stations (replicates) | level of openness to the sea |
|---|---|---|---|
| Kristiansand (Topdalsfjord) | KI | 12-15-16-17 | half closed |
| Høvåg (Steindalsfjord) | HO | 33-36-37-39 | half closed |
| Sandnesfjord, Risør[a] | SA | 91-92-94-95 | half closed |
| Søndeledfjord, Risør | SO | 111-112-121-122 | half closed |
| Kragerø area | KR | 161-163-164-182 | half closed |
| Grenlandfjord Inner | GI | 191-192-194-195 | half closed |
| Grenlandfjord Entrance | GE | 198-199-200-202 | half closed |
| Tjøme[a] | TJ | 232-233-234-238 | open |
| Holmestrand fjord | HF | 251-252-253-254 | half closed |
| Inner Oslofjord[a] | IO | 291-292-293-295 | closed |
| Drøbak area | DR | 321-322-326-327 | half closed |
| Hvaler[a] | HV | 342-343-344-345 | open |

[a] More sampling stations were available for these locations. The four stations used in the analyses are chosen at random.

munities are related to their relative spatial location. As a result of this we aim at testing whether communities exposed to the open sea are less variable than communities in more sheltered areas and whether exposed communities are similar to each other.

## 4. ANALYSES

### (a) *Estimating parameters of fish communities*

The community data from the Norwegian Skagerrak coast permit us to apply a method specifically developed for situations for which the probability of detecting a species varies among species (Burnham & Overton 1979). The jackknife estimator of species richness proposed by Burnham & Overton is known to be fairly robust to potential departures from model assumptions (e.g. spatial heterogeneity in detection probability among sampling replicates), as shown both through various simulations (e.g. Burnham & Overton 1979; Heltshe & Forrester 1983; Baltanas 1992; Poulin 1998; Walther & Morand 1998) as well as through empirical (Palmer 1990) studies.

Estimates of temporal change of communities (local rate of change in species richness, rate of local extinction and rate of local turnover) were obtained following Nichols *et* *al.* (1998*a*). The rate of change in the number of species between two consecutive years ($S_t/S_{t-1}$) is the number of species present one year ($t$) divided by the number of species present the year before ($t - 1$). The local extinction probability ($E$) between two years is defined as the proportion of species lost from the community between two consecutive years (Nichols *et al.* 1998*a*), while the rate of turnover ($T$) is defined to be the proportion of species that were not present the previous year (Nichols *et al.* 1998*a*). Note that the rates of local extinction and turnover deal with changes in the species composition of the community.

If the community is close to equilibrium, the rate of change will be close to zero. The rates of local extinction will then be approximately equal to the turnover rate (i.e. proportion of new species in the community). To test whether species richness maintained a constant size over the study period, the means of the yearly rates of change in species richness (measured as $\log(\hat{S}_t/\hat{S}_{t-1})$) of each community were computed and compared with zero. If $\hat{S}_t/\hat{S}_{t-1}$ is different from zero, we can investigate possible mechanisms using $\hat{E}$ or $\hat{T}$.

The repeated sampling of the fjord communities permits us to define two levels of sampling and thus to estimate the community parameters referred to in the previous paragraph. We define the primary sampling session as sampling over an area corresponding to a given community for each year (i.e. the fjord). The secondary sampling sessions are then the spatial sampling replicates within that area (i.e. sampling stations within a fjord for a given year). For each pair of primary sampling sessions, the respective number of species observed at exactly $i$ of the sampling stations ($f_i$) and the total number of species detected at each sampling station ($n_i$) were first obtained, and then used in further computations.

Estimates of spatial change between communities (turnover of species between area $j$ and area $i$) were computed following Nichols *et al.* (1998*b*). These estimates allowed us to compare the composition of the communities at different locations.

We used the software Comdyn (Hines *et al.* 1999; http://www.mbr-pwrc.usgs.gov/comdyn.html) that permits computation of the jackknife richness estimator of Burnham & Overton (1979) and of the estimators of rate of increase in species richness, local extinction and turnover, as described by Nichols *et al.* (1998*a*). The standard errors of the estimates were obtained using a bootstrap approach (Hines *et al.* 1999; see Nichols *et al.* (1998*a*) for a description of the variance estimation procedure).

### (b) *Analyses of the spatio-temporal patterns of community change*

The resulting time-series estimates of fish species richness were used as a basis for investigating the spatio-temporal dynamics of fish communities along the Norwegian Skagerrak coast.

#### (i) *Temporal and spatial change in species richness*

Analyses of covariance (ANCOVAs) were carried out to test for the presence of linear trends and differences in average values (especially for the heavy polluted Holmestand fjord and the two Grenland areas; Johannessen & Dahl 1996; see figure 1) of the various estimates for each area over the considered period.

The amount of temporal variability of species richness over the study period was studied by computing the coefficient of variation ($\mathrm{CV}(S_i)$) of species richness (taking sampling error into account; see Link & Nichols 1994). The variance of a temporal sequence of point estimates of species richness may be expressed as the sum of two variance components, one of which is related to ecological processes ('true' temporal variance in species richness) and one which is related to the sampling process (sampling variance associated with the estimation process). Here, we used a method designed to separate these components (Burnham *et al.* 1987; Skalski & Robson 1992; Link & Nichols 1994). This method has earlier been used to estimate temporal variability in the species richness of bird communities (Boulinier *et al.* 1998).

To identify and explore the dominant modes of variation of species richness across space, we used principal component analysis (PCA; Legendre & Legendre 1983; Manly 1994; Fromentin *et al.* 1997; Lekve *et al.* 1999).

#### (ii) *Temporal and spatial change in composition*

The estimates of year-to-year rates of local extinction probability ($\hat{E}$) and turnover ($\hat{T}$) were computed for each fjord or area. ANCOVAs were carried out to test for the presence of linear trends and differences in mean values of these estimates for each area over the considered period.

## 5. RESULTS

### (a) *Species detectability and sampling variability*

Using the patterns of detection–non-detection of 34 species after 1952 within 12 fjords (with four stations as replicates for each community), we estimated average species richness over all communities of 16.38 (figure 2) and a mean average detection probability of 75.39% (averaged over communities as detection probability did not vary among years or localities). The values of the average detection probability (over four replicates) imply that the probability of detecting that a given species is present is *ca.* 30% per sampling station (as the average probability for a species of being detected at each of the four sampling stations is *ca.* 0.3, the probability of being missed at each of the four sampling stations is 0.7, it leads to an overall probability of being missed at all four stations of $[0.7]^4 = 0.24$, and thus to an overall probability of detection of *ca.* 75%). Sampling variance may thus explain a large part of the variability in both observed and estimated species richness. No difference in average detection probabilities was found either among localities or among years ($n = 526$ year locality, ANCOVA locality: $F_{11,502} = 1.13$, $p = 0.33$, year: $F_{1,502} = 0.04$, $p = 0.84$, locality × year: $F_{11,502} = 1.09$, $p = 0.37$).

### (b) *Spatial scale of variation in species richness and community composition*

After removing three outliers of a total of 514 (Kragerø 1974, Grenland Inner 1987 and Grenland Inner 1988; Cook's distance of greater than 0.2; Sen & Srivastava 1990), average species richness was found to differ among the 12 fjord-based communities (ANCOVA; $F_{11,510} = 5.76$, $p < 0.01$), with the lower values occurring in the two

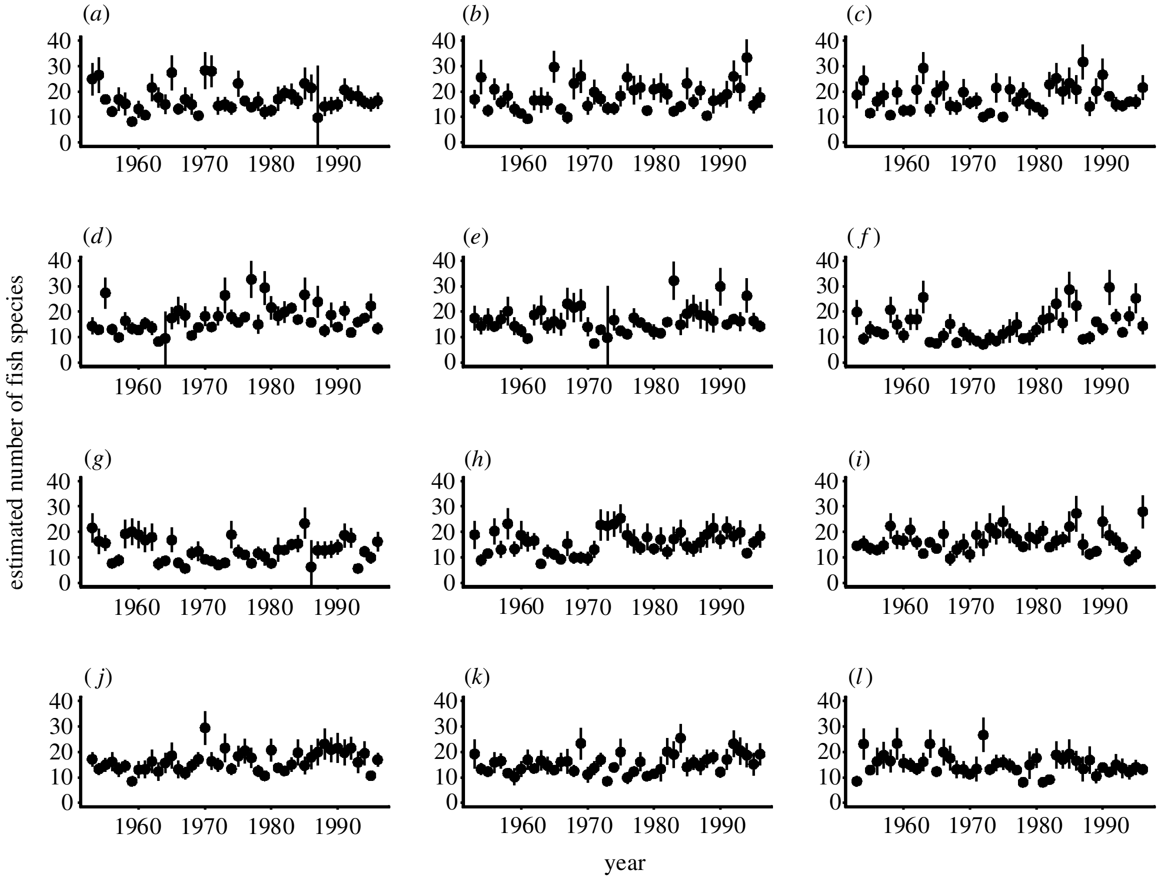

Figure 2. Time-series of the estimated species richness with associated standard errors for the 12 study areas situated along the Norwegian Skagerrak coast (jackknife estimates based on four spatial replicates per community). (*a*) Kristiansand, (*b*) Høvåg, (*c*) Sandnesfjord, (*d*) Søndeledfjord, (*e*) Kragerø, (*f*) Grenlandfjord Entrance, (*g*) Grenlandfjord Inner, (*h*) Tjøme, (*i*) Holmestrand fjord, (*j*) Hvaler, (*k*) Drøbak area, (*l*) Inner Oslofjord.

communities of the Grenland fjords, and the higher values occurring in the communities of Høvåg, Sandnesfjord and Søndeledfjord (table 2). A multiple test of differences between the locations using comparison-wise errors ($p < 0.05$) shows that the estimated number of species in the Inner Grenland fjord was significantly lower than the estimates in the other areas. Among the rest of the locations, the estimated number of species at the entrance region of the Grenland fjord is significantly lower than the estimate of other fjords except for those of the Drøbak area and Inner Oslofjord. There was a slight but significant linear increase in the estimated species richness for all communities over the study period ($F_{1,510} = 11.81$, $p < 0.01$, multiple $R^2 = 0.13$) without any interaction between the year and community ($F_{11,499} = 1.34$, $p = 0.20$).

The estimated spatial parameters comparing the fjords—the turnover of species between fjord $j$ and fjord $i$ ($\hat{T}_{ij}$)—were used to assess differences in the composition of the communities among the fjords. The estimates comparing the composition among communities (not shown) take by and large higher values than the means of the year-to-year estimates of the change in composition within communities (mean $\hat{T}$ between 0.19 and 0.24; table 2). Also, a higher proportion of these estimates were significantly greater than 0 when comparing the composition of various communities than for year-to-year comparisons of change in composition (percentage turnover greater than 0; table 2).

### (c) *Temporal patterns of change in community dynamics and species richness*

Temporal variability of species richness within each community was measured as $\hat{\mathrm{CV}}(S_i)$, estimated as the ratio of the square root of the estimated true temporal variance over the mean of the species-richness estimates. This measure properly accounts for sampling variation and focuses on true temporal variation in species richness. The values of $\hat{\mathrm{CV}}(S_i)$ attained were between 10 and 20%, except for the two communities of the Grenland fjords, which had values of more than 30% (table 2). The two Grenland communities thus showed more temporal variability in species richness over the period than did the other areas. This can be explained by the strong decreasing trend in species richness exhibited by both Grenland communities between 1952 and 1970 (ANCOVA; effect of the year: $F_{1,31} = 4.09$, $p = 0.05$). Conversely, for the period between 1970 and 1997, the community inside the Grenland fjords exhibited no trend in species richness ($F_{1,25} = 0.8$, $p = 0.38$), whereas the community at the entrance of the Grenland fjords exhibited an increasing linear trend ($F_{1,25} = 10.42$, $p = 0.0035$; figure 2). It should also be noted that the community of the inside of the Oslofjord had the lowest CV of the species richness (table 2 and figure 2).

The mean yearly rate of local extinction is estimated to be between 19 and 25% (table 2), showing no evidence of a difference in the mean rate of local extinction among

Table 2. Mean species richness (mean $\hat{S}$), temporal variation in species richness ($\hat{\mathrm{C}}\mathrm{V}(S)$), mean of the log of the year-to-year local rate of increase in species richness (mean $\log(\hat{S}_j/\hat{S}_i)$), and mean of the year-to-year rate of local extinction (mean $\hat{E}$) and rate of local turnover (mean $\hat{T}$) for the 12 study areas over the study period.
($\hat{\mathrm{C}}\mathrm{V}(S)$ is the coefficient of the temporal variation of species richness computed taking sampling variance into account. Replication-based standard errors of the means of these variables are given, as well as the percentage of year-to-year local extinction and year-to-year local turnover that were significantly different from 0 using the 95% bootstrap confidence interval ($\%\hat{E} > 0$ and $\%\hat{T} > 0$). The number of years ($n$) over which the parameters were computed is also reported.)

| community | abbreviation | $n$ | mean $\hat{S}$ | (s.e.) | $\hat{\mathrm{C}}\mathrm{V}(S)$ | mean log $(\hat{S}_j/\hat{S}_i)$ | (s.e.) | mean $\hat{E}$ | (s.e.) | $\%\hat{E} > 0$ | mean $\hat{T}$ | (s.e.) | $\%\hat{T} > 0$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Inner Oslofjord | KI | 52 | 14.381 | 0.566 | 9.98 | −0.0054 | 0.05568 | 0.2439 | 0.01761 | 7.7 | 0.2425 | 0.01799 | 15.4 |
| Drøbak area | HO | 52 | 15.155 | 0.588 | 12.74 | −0.0160 | 0.04838 | 0.1979 | 0.01601 | 9.6 | 0.2085 | 0.01881 | 15.4 |
| Holmestrand fjord | SA | 52 | 15.250 | 0.599 | 11.21 | 0.0078 | 0.04949 | 0.1911 | 0.01534 | 5.8 | 0.1899 | 0.01361 | 1.9 |
| Tjøme | SO | 52 | 14.566 | 0.672 | 16.88 | −0.0107 | 0.05662 | 0.2179 | 0.01567 | 5.8 | 0.2245 | 0.01611 | 3.8 |
| Hvaler | KR | 52 | 15.657 | 0.576 | 10.09 | −0.0011 | 0.04243 | 0.1973 | 0.01633 | 7.7 | 0.2013 | 0.01632 | 13.5 |
| Grenlandfjord Inner | GI | 44 | 11.462 | 0.755 | 32.15 | −0.0151 | 0.08340 | 0.2381 | 0.02295 | 13.6 | 0.2269 | 0.02203 | 6.8 |
| Grenlandfjord Entrance | GE | 44 | 13.448 | 0.903 | 30.71 | −0.0098 | 0.07213 | 0.2290 | 0.01947 | 6.8 | 0.2336 | 0.01963 | 11.3 |
| Kragerø area | HV | 50 | 15.824 | 0.751 | 17.07 | 0.0138 | 0.05745 | 0.2243 | 0.01561 | 10.0 | 0.2353 | 0.01793 | 14.0 |
| Søndeledfjord, Risør | HF | 52 | 16.597 | 0.696 | 20.54 | −0.0066 | 0.05441 | 0.2088 | 0.01794 | 7.7 | 0.2103 | 0.01963 | 9.6 |
| Sandnesfjord, Risør | IO | 52 | 16.799 | 0.677 | 14.68 | 0.0020 | 0.05687 | 0.1910 | 0.01543 | 9.6 | 0.1945 | 0.01615 | 11.5 |
| Høvåg (Steindalsfjord) | DR | 52 | 17.188 | 0.804 | 21.22 | −0.0165 | 0.06233 | 0.1995 | 0.01927 | 13.5 | 0.2048 | 0.01773 | 13.5 |
| Kristiansand (Topdalsfjord) | TJ | 44 | 15.762 | 0.761 | 17.49 | 0.0016 | 0.05964 | 0.2428 | 0.02188 | 11.4 | 0.2370 | 0.01964 | 11.4 |

communities; nor any within-community linear trend. The mean yearly rate of local turnover was also estimated to be between 19 and 25% (table 2), showing neither any temporal trend nor any spatial structure (no differences).

In contrast to the patterns found for species richness (see previous paragraph) and contrary to our expectations, no trends were found in the community dynamics parameters when the data were split into periods before and after measures against pollution were undertaken (i.e. somewhat arbitrarily set to pre- and post-1970) either for local extinction or for turnover rates.

It should be noticed that the means of the year-to-year rates of local extinction and the mean year-to-year rates of local turnover had comparable values for each area: this was in concordance with the lack of any evidence of a consistent increase or decrease in species richness within each community over the study period (figure 2 and table 2).

### (d) *Spatio-temporal patterns of species richness*

In order to analyse the spatio-temporal patterns further, we performed a PCA on the estimated species richness (on log-scale) from 1953 to 1996, removing three low values in 1974, 1987 and 1988 of the Kragerø area (the first) and the inner Grenland area—recognized as outliers (see § 5b). The three axes of the PCA capture 47% of the variability in the data. The main pattern (i.e. the principal axis) of temporal variability (explaining 19%) displays an initial decrease in the species richness followed by a recovery during the 1960s and a stabilization during the 1970s (figure 3*a*). Five areas display positive (and high) scores for this temporal pattern (to the right in figure 3*d*,*e*). Using the (independent) values of exposure of each station, the stations within the five areas are significantly more exposed than the stations within the other seven areas (mean exposure of 2.45 and 1.70, respectively, $t$-value = 1.95, $p < 0.05$), supporting our prediction of a similarity in the temporal pattern of species richness in exposed areas. The second axis of variation displays a decrease until the early 1970s followed by an increase (explaining 17% of the total variability; figure 3*b*) without any interpretable spatial pattern (figure 3*d*, *f*). The first and second principal axes taken together separate the Inner Oslofjord from the rest of the areas ('IO' located in the lower left corner of figure 3*d*). The third axis displays a decrease in the early period followed by fluctuations (explaining 12% of the total variability; figure 3*c*), linking the polluted Grenland fjords with the Holmestrand fjord (high values in figure 3*e*, *f*).

Overall, the PCA supports a possible relationship between the level of exposure and temporal variation in species richness. Furthermore, the PCA distinguishes polluted areas (Johannessen & Dahl 1996) in which the estimated number of species exhibit a temporal pattern that is different from that of the other communities during the study period (i.e. the two Grenland fjord communities, the Holmestrand fjord and the Inner Oslofjord area).

## 6. DISCUSSION

Along the Norwegian Skagerrak Coast (covering *ca.* 210 km), heterogeneity was found among fjords with respect to fish species richness. With this study we provide

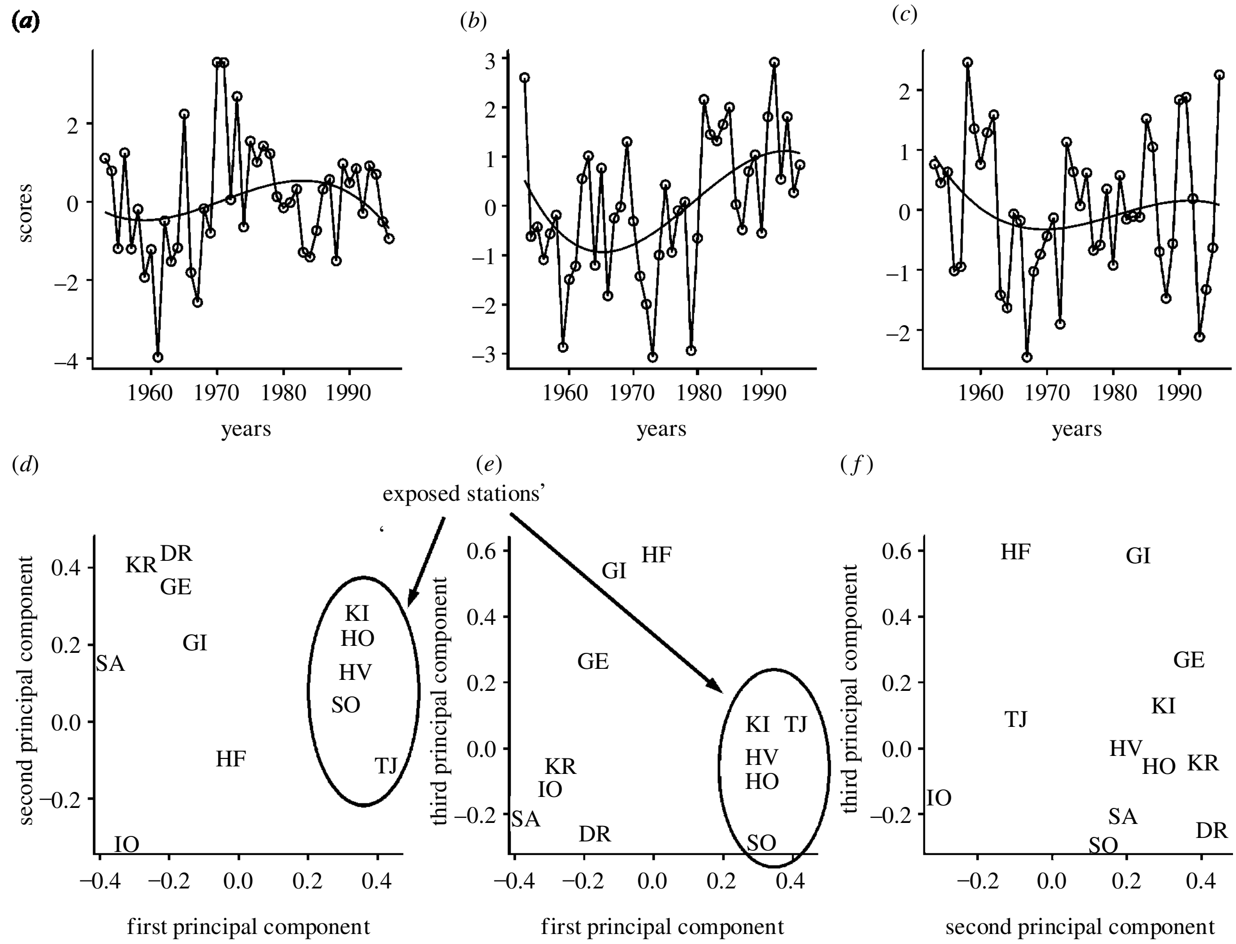

Figure 3. PCA of the 12 study areas of the estimated number of species over 1953–1996 performed on the species-richness data (on a log scale): the most important axes of variation of the species richness (accounting for 19, 17 and 12% of the variability in the data, respectively). (*a*) First principal component, i.e. the primary temporal pattern of variability of the PCA, corresponding to the mean number of species per year (on a log scale). (*b*) Second principal component. (*c*) Third principal component. A third-order polynomial is fitted to the temporal patterns to highlight the shape of the temporal patterns. (*d–f*) Score plot displaying the scores of the stations on the first three axes of variability. (*d*) First principal component versus second principal component. (*e*) First principal component versus third principal component. (*f*) Second principal components versus third principal components. Abbreviations as in table 1.

support for previously expected patterns in species richness (e.g. low richness in polluted areas; table 2) as well as establish the presence of patterns previously not shown (i.e. difference in temporal patterns of species richness between exposed and sheltered areas; figure 3). Our analyses have furthermore demonstrated that local variability creates differences between fjords, while the exposure to the open sea plays a homogenizing role on a larger spatial scale. Our analyses thus demonstrate that *both* local and regional processes are of significance for fish-community species richness and composition.

Less structure was found in the temporal variability. Only the CV was higher for fjords predicted *a priori* to be disturbed (i.e. the Grenland fjords). Notice, however, that two other fjords predicted *a priori* to be disturbed (i.e. the Holmestrand area and the Oslofjord), displayed low coefficients of variation.

The Norwegian Coastal Current (NCC; Danielssen *et al.* 1996, 1997) is likely to impose large-scale homogenization of the fish community processes along the Norwegian Skagerrak coast. This current has lower salinity than the basin water masses due to freshwater outflow from the Baltic Sea and flows counter clockwise along the Skagerrak basin. The difference in salinity stabilizes the water masses and creates an enduring pycnocline. Such a stable stratification facilitates richer plankton growth in areas exposed to the open sea than in the more sheltered areas (Gjøsæter *et al.* 2000). Other unique properties of the current, and the advective transport of individuals of species from the coastal seawater species pool (see Roughgarden *et al.* 1994), might also contribute to reducing the variability among areas along the coast. Finally, properties important for metabolic activity, such as temperature, salinity and oxygen saturation might contribute to differentiating exposed areas from the more sheltered ones (Wootton 1990).

The degree of exposure is not solely responsible for differences in species-richness dynamics. Over a period of several decades, one would expect that even stationary fish species within fjords would have an opportunity to become widely dispersed along the coast. The variability within fjords is a function of local variability in, for example, habitat structure and niche availability, and the coastal current is one of the factors distinguishing habitats close to the open sea from protected habitats. This is, of course, indirectly related to exposure, but the connections remain a complex issue.

On the local scale, our analyses demonstrated that several areas differed from the other areas in species diversity. However, there seem to be different mechanistic explanations for the uniqueness of the different areas. Community dynamics of the Inner Oslofjord seems to be independent of the other communities; with a relatively low number of species, this community exhibits a different pattern of temporal change (figure 3), and a consistently higher proportion of species were absent in this region compared with others (not shown). The relatively large size of the Oslofjord (*ca.* 50 km) and the bathymetry (the area is enclosed by a shallow sill), probably play an important role in this context (Lekve *et al.* 1999). For the Holmestrand fjord and the two communities in the Grenland fjord pollution has probably been a key factor (Follum & Moe 1988; Johannessen & Dahl 1996). The latter areas showed significantly lower mean species richness and higher temporal variability in species richness. These two communities are situated inside and at the entrance of the Grenland fjords. The first one showed consistently low species richness until 1997, while the second one showed an increase in species richness over the second half of the study period. This may correspond to a re-invasion facilitated by the direct exposure to the Skagerrak Sea. The recovery of the entrance area of the Grenland fjord area is another indication of the importance of exposure to the open Skagerrak Sea. The Grenland fjords (especially the inner area) are thus characterized by a low, stable diversity with few species able to colonize niches in the community.

Altogether, by incorporating sampling variability, we have been able to obtain estimates of community-dynamics parameters for fish communities (indicating that the fjord is an appropriate unit for studying processes of coastal fish dynamics in space and time). These parameters seem to represent the processes in the coastal zone in a successful manner, demonstrating high consistency in processes of local extinction and turnover. Furthermore, the obtained estimates demonstrated geographical differences in richness. Both the differences in species richness and the similarity in dynamic properties in the communities indicate that external factors are most likely to be responsible for regional differences in richness. Two such processes may be identified from our analysis—the homogenizing role of currents (the NCC) and the differentiating role of local pollution.

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