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## Modeling species richness controlled by community-intrinsic and community-extrinsic processes: coastal fish communities as an example

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**Abstract** This article focuses on the analysis of coastal fish communities along the Norwegian Skagerrak coast. Species numbers are estimated based on annual samples of the fish communities within 12 fjords from 1953 to 1994. On this basis, a community dynamics model (incorporating both community-intrinsic and community-extrinsic processes) was developed and analyzed. This model is then discussed on the basis of other community models available through the literature, both phenomenologically oriented and process-oriented models.

**Key words** Settlement · Local extinction · Equilibrium · Nonequilibrium · Regulation · Macroecology

### Introduction

The biodiversity of ecological communities plays a vital role for ecosystem functioning in a changing environment (Begon et al. 1990; Gaston 1996, 2000). Any community's biodiversity is – on a shorter ecological time scale – an emergent property of ecological processes such as colonization and settlement as well as (local) extinction (Brown 1995) and – on a longer evolutionary time scale – an emergent property of speciation as well as colonization followed by settlement and extinction (Stenseth and Maynard Smith 1984). Within an ecological setting, such as the one adopted in this article, species diversity depends upon ecosystem

characteristics such as vegetation, soil, climate, and disturbance regimens (Paine 1966; MacArthur and Wilson 1967; MacArthur 1972; Diamond and Cody 1975; Rosenzweig 1995; Kerr and Currie 1999; Brown and Lomolino 2000; Loreau 2000; Pianka 2000; Brown et al. 2001; Loreau and Hector 2001a,b; Loreau et al. 2001; Lekve et al. 2002d).

Much of the literature on community dynamics adopts an equilibrium point of view. However, an ecological system may be heavily influenced by substantial stochasticity, as well as nonlinearities, making the resulting system a nonequilibrium one. In marine systems, a theoretical framework emphasizing the high level of stochasticity, creating nonequilibrium states (cf. Murdoch 1994), may be required. Steele (1985) suggested that marine, as opposed to terrestrial, ecological systems are likely to “show longer term changes between alternative community structures.” Marine systems are thus expected to be of a nonequilibrium type (Murdoch 1994) and characterized by either switching between two or more equilibrium conditions or profoundly affected by stochasticity.

The biological responses of marine systems to environmental perturbations may be discussed in terms of their obvious high degree of resilience (i.e., the ability to recover from a high level of stress) and stability (i.e., a fast rate of recovery following a perturbations), although having a lower degree of inertia (i.e., a weak ability to withstand perturbation; also known as “resistance” or “persistence”) (Holling 1973; Pimm 1986; Underwood 1989, 1999). For a system to be of a nonequilibrium type, non-linearity is required, which is likely to be the case for the particular systems we are considering (Bjørnstad et al. 1999b). Equally important is the presence of a high level of stochasticity, which is likely to be the case for marine systems (Hjort 1914; Cushing 1990, 1996; see also Stenseth et al. 1999).

Population dynamics is well studied and has developed into a firm theory structure (May 1981). No similar theoretical platform exists for community dynamics: at best, only fragments for such a theory exist (Brown et al. 2001). In this article, we provide an empirically based contribution to such a theory development. Rather than developing a mathematically elegant theory with many untested assumptions,

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we take the approach of “asking” data on a coastal fish community, that is, what such a theory might look like. Such an approach has proved valuable in connection with population dynamics questions (Stenseth 1999; Stenseth et al. 1997, 1999).

Here we specifically discuss a model developed to understand the dynamics of the species diversity within local (and coastal) marine fish communities (Lekve et al., unpublished). This model aims at understanding the patterns discussed within the field of macroecology (*sensu* Brown 1995) as emergent results of community processes (such as colonization and settlement, and local extinction). An overall objective of the paper is to assess the validity of such a model (Lekve et al., unpublished) by simplifications and reformulations of the basic model as well as to relate it to other available models in the literature. By applying different modeling approaches, we provide a sound basis for discussing possible extensions of the modeling of community dynamics.

## The system

We consider coastal fish communities along the Norwegian Skagerrak coast (Fig. 1). This is an open system characterized by extensive mixing of water masses (Danielssen et al. 1996, 1997). The overall species pool (the complete list of species) is shown in Table 1. Our discussion will be generally applicable to any ecological community being characterized by species continuously becoming locally extinct, after which they may reinvade (from some large species pool) and settle in the community, all of which

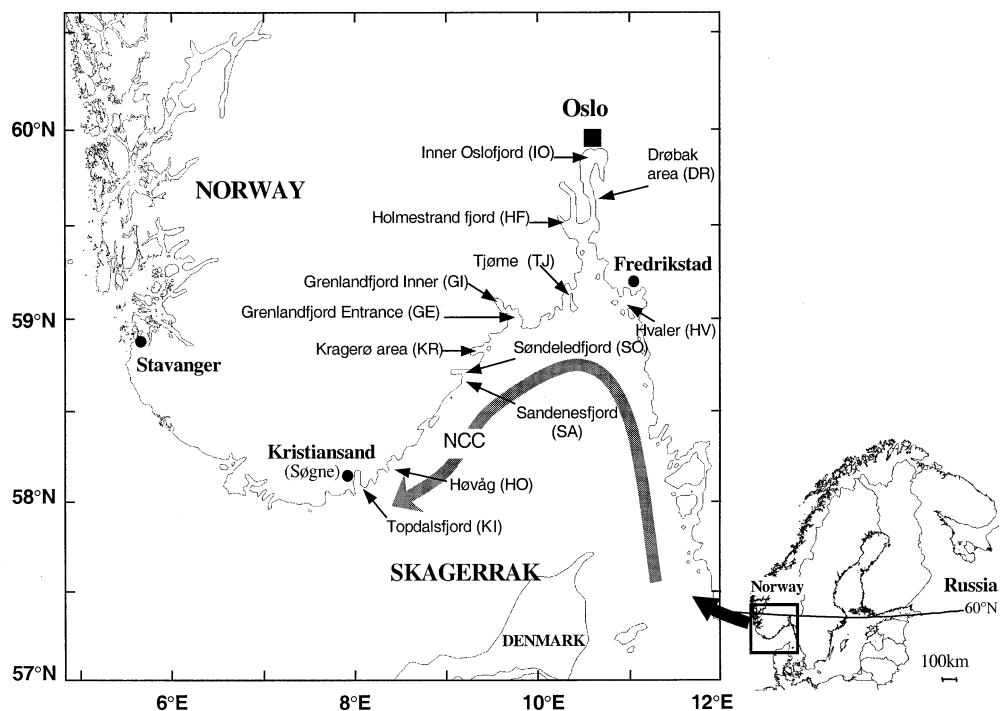
being influenced by abiotic factors (such as climate) and biotic factors (such as competition for space and food resources).

Because of the properties of the ocean (weak geographic barriers) and the strong dispersal ability of fish (buoyancy of egg and/or larva, spawning migrations), the habitats of fish in the coastal zone along the Norwegian Skagerrak coast may be described as non-isolated habitats. As most fish have a great recruitment potential (e.g., a female cod may spawn 5 million eggs; Kjesbu et al. 1996) and currents are present along the coast, we may assume that there is a constant supply of potential colonists from the open sea to vacant niches in each of the fjords (Fig. 2). In our setting (see following), the impact of the two processes determining species richness in the classical island biogeographic setting – distance and size of the habitat – are of minor importance to the dynamics of the number of species in the fjord community.

## The basic community data

More than 250 stations between Kristiansand and the Norwegian–Swedish border have regularly been sampled during September–October since 1919 by beach seine hauls; about 100 are still being sampled (see Fig. 1). The 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 person counting and classifying the species; since 1919 there

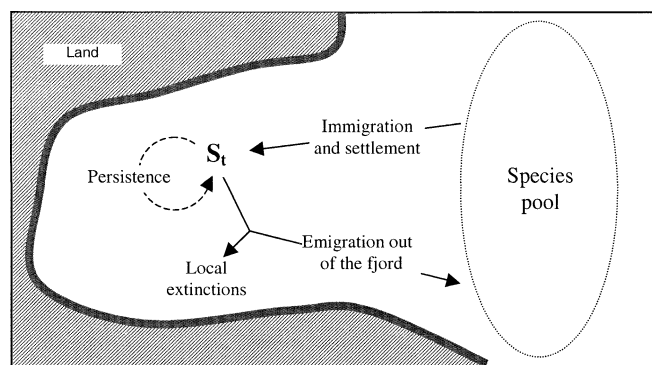
**Fig. 1.** Location of the Norwegian Skagerrak coast. Since 1919, permanent localities along the coast between Kristiansand and Fredrikstad have been sampled by beach seine each autumn, using a highly standardized methodology with only two leaders of the expedition since the start. About 100 stations are still sampled, and 34 species of fish has been registered. (See Fromentin et al. 1997; Lekve et al. 1999 for a more detailed description of the monitoring program). Labeled in the main figure are the 12 fjords/areas for which at least 4 replicates (i.e., stations) exist. Along the Norwegian Skagerrak coast floats the Norwegian Coastal Current, *NCC* (shaded arrow)



**Table 1.** The species included in this analysis of the Flødevigen data

Common name	Latin name
Fish species with numerical counts (21 species)	
Cod	<i>Gadus morhua</i> Linnaeus, 1758
Whiting	<i>Merlangius merlangus</i> (Linnaeus, 1758)
Saithe (pollack)	<i>Pollachius virens</i> (Linnaeus, 1758)
Pollack	<i>Pollachius pollachius</i> (Linnaeus, 1758)
Sea trout	<i>Salmo trutta</i> Linnaeus, 1758
Eel	<i>Anguilla anguilla</i> (Linnaeus, 1758)
Ballan wrasse	<i>Labrus bergylta</i> Ascanius, 1767
Haddock	<i>Melanogrammus aeglefinus</i> (Linnaeus, 1758)
Mackerel	<i>Scomber scombrus</i> Linnaeus, 1758
Plaice	<i>Pleuronectes platessa</i> (Linnaeus, 1758)
Lemon Sole	<i>Microstomus kitt</i> (Walbaum, 1792)
Turbot	<i>Scophthalmus maximus</i> (Linnaeus, 1758)
Brill	<i>Scophthalmus rhombus</i> (Linnaeus, 1758)
Norwegian topknot	<i>Phrynorhombus norvegicus</i> (Guenther, 1862)
Common topknot	<i>Zeugopterus punctatus</i> (Bloch 1787)
Sole	<i>Solea vulgaris</i> (Quensel, 1806)
Cuckoo wrasse	<i>Labrus bimaculatus</i> (Linnaeus, 1758)
Dragonet	<i>Callionymus lyra</i> Linnaeus, 1758
Armed bullhead	<i>Agonus cataphractus</i> Linnaeus, 1758
Rock gunnel	<i>Pholis gunnellus</i> (Linnaeus, 1758)
Grey gurnard	<i>Eutrigla gurnardus</i> (Linnaeus, 1758)
Fish species with categorical counts (13 species)	
Herring	<i>Clupea harengus</i> Linnaeus, 1758
Sprat	<i>Sprattus sprattus</i> (Linnaeus, 1758)
Horse mackerel	<i>Trachurus trachurus</i> (Linnaeus, 1758)
Flounder	<i>Platichthys flesus</i> (Linnaeus, 1758)
Dab	<i>Limanda limanda</i> (Linnaeus, 1758)
Long rough dab	<i>Hippoglossoides platessoides</i> (Fabricius, 1780)
Goldsinny wrasse	<i>Ctenolabrus rupestris</i> (Linnaeus, 1758)
Corkwing wrasse	<i>Crenilabrus melops</i> (Linnaeus, 1758)
Rock cook	<i>Centrolabrus exoletus</i> (Linnaeus, 1758)
Threespine stickleback	<i>Gasterosteus aculeatus</i> Linnaeus, 1758
Fifteenspine stickleback	<i>Spinachia spinachia</i> (Linnaeus, 1758)
Poor cod	<i>Trisopterus minutus</i> (Linnaeus, 1758)
Viviparous eelpout	<i>Zoarces viviparus</i> Linnaeus, 1758

Taxonomy according to The Integrated Taxonomic Information System (ITIS) at web site <http://www.itis.usda.gov/index.html>



**Fig. 2.** Schematic overview of some assumptions and processes taking place in fish communities in the coastal zone along the Norwegian Skagerrak coast.  $S_t$  is the number of species at time  $t$

have been only two leaders (Stenseth et al. 1999). The Flødevigen monitoring data include a total of 59 species and groups of species.

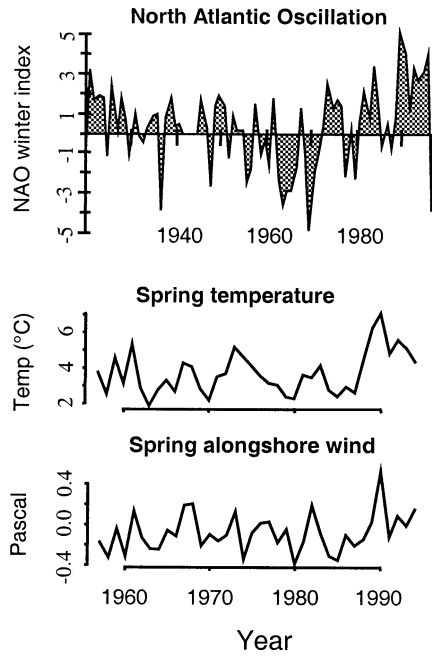
Only fish species are included, leaving a total of 34 fish species as input for the estimation of community dynamics (Lekve et al. 1999; see Table 1). Some of the fish species use the coastal zone as a nursery area [e.g., the gadoids, such as

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 life in the coastal zone. From release–recapture studies it is known that the cod is highly stationary at a scale smaller than the fjord (Julliard et al. 2001), and this is also the observation for most other species (A. Sollie, personal communication).

Because our environmental data are complete only from 1957 (Fig. 3), the analyses represented here cover 1957 to 1994.

### Species richness

The probability of detecting a certain fish species varies among species (Burnham and Overton 1979). We have used multiple sampling on a fjord scale to account for non-detectability and sampling variability. By applying the DOS version of software COMDYN (Hines et al. 1999) (<http://www.mbr-pwrc.usgs.gov/comdyn.html>), which permits computation of the jackknife estimator of Burnham and Overton (1979), we constructed time series for each of the



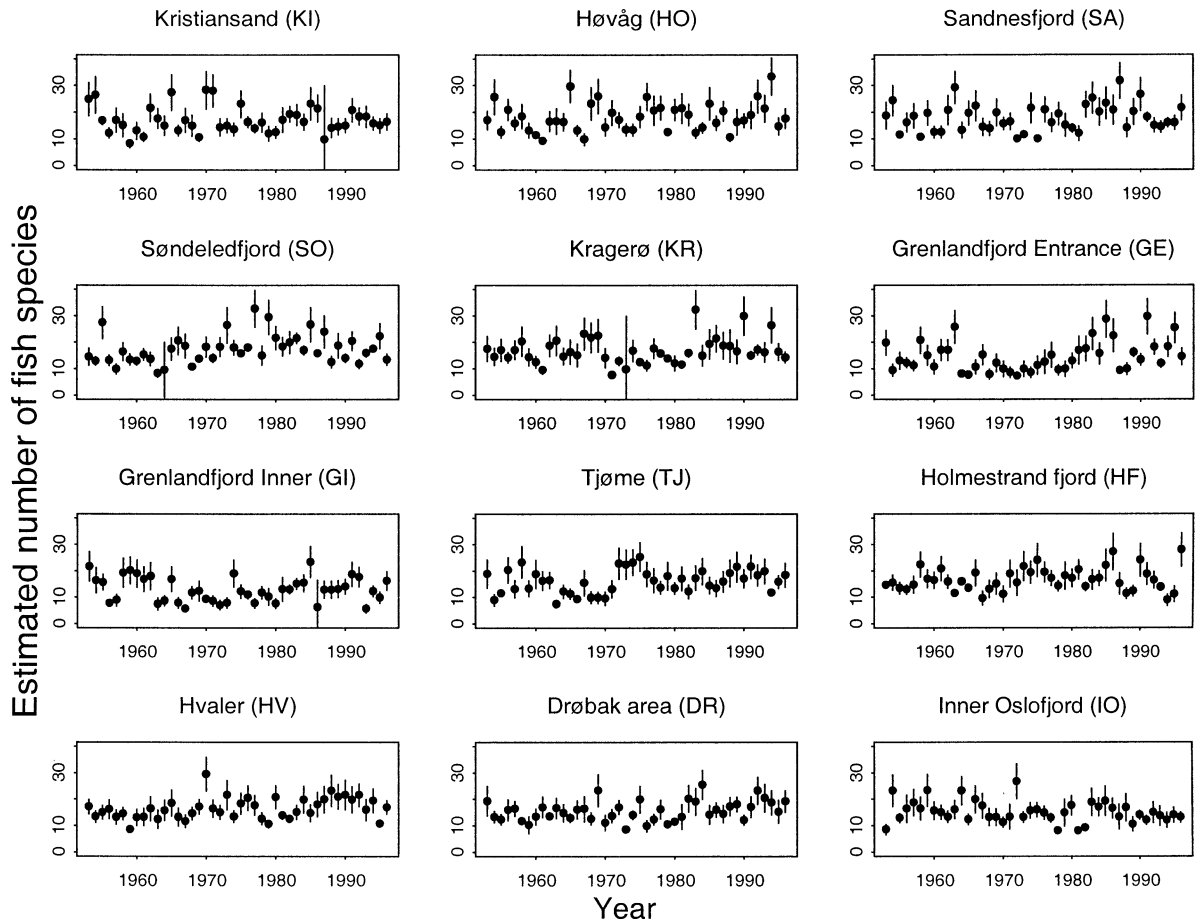
**Fig. 3.** Time series of the North Atlantic Oscillation 1919–1994 (*top*) (NAO; Hurrell 1995), mean spring temperature (March and April) at 1 m depth (*middle*) and mean spring alongshore wind stress (*bottom*) (March and April) 1957–1994 (see Lekve et al. 2002b)

12 fjords/areas based on four stations within each location (Lekve et al. 2002a). The standard errors of the estimates were obtained using a bootstrap approach (Hines et al. 1999; see Nichols et al. 1998 for a description of the variance estimation procedure).

The data are plotted in Fig. 4. As can be seen, there is some temporal variability. Our overall purpose here is to model this temporal variability in each of the fjords, and then to try to understand the spatial variations in this temporal structure.

Climatic variables

For coastal systems, such as the one analyzed in this study, patterns of currents and temperature influence the growth and survival of fish (Wootton 1990; Mann and Lazier 1991). Along the Norwegian Skagerrak coast, wind stress in the spring (Ottersen and Sundby 1995; Lekve et al. 2002b) seems to be a good proxy for the advective processes influencing recruitment (Lekve et al. 2002b). The wind was decomposed into alongshore wind stress (Ottersen and Sundby 1995; Lekve et al. 2002b). As the main period of recruitment for the most abundant species, the gadoids, is in the spring, wind and temperature were averaged



**Fig. 4.** Time series of 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)

over March and April (Lommond et al. 1998; Lekve et al. 2002b). The influence of environmental conditions on species richness a given year is probably not limited to the same year. However, the indirect influence of environmental conditions in the previous year(s) will most likely be highly diluted. Some indirect proxy measure of climate such as the North Atlantic Oscillation (NAO; Hurrell 1995; see Fig. 3) might represent past environmental variability in a satisfactory manner. The NAO reflects the difference in surface level air pressure between the high-pressure zone concentrated around the Azores and the low-pressure zone over Iceland. The NAO winter index is strongly correlated with local environment (Fromentin et al. 1997; Hurrell and van Loon 1997; Ottersen et al. 2001), and is thus a predictor of localized climatic variability that influences the growth and survival of fish. For our study area, the effect of weather on species richness is thus composed of wind stress and temperature in the present year and the North Atlantic Oscillation in the present and previous year as possible influential factors. Data on the North Atlantic Oscillation Winter Index are available from the Internet site [www.cgd.ucar.edu:80/~jhurrell/nao.html](http://www.cgd.ucar.edu:80/~jhurrell/nao.html). Data on wind and sea surface temperature were obtained from the Norwegian Meteorological Institute (for details, see Fromentin et al. 1998; Lekve et al. 2002b).

The environmental variables are displayed in Fig. 3. The environmental variables are strongly correlated (correlation coefficient between NAO and temperature, 0.76, and between NAO and wind stress, 0.43), and the temperature and wind stress can be reasonably well expressed as a linear function of the NAO values (Fig. 5).

## An empirically based community model

### The model

Fundamentally, the number of species in a fjord is determined by recruitment [i.e., immigration and settlement; the function  $R(\bullet)$ ] and persistence [the function  $P(\bullet)$ ] of species, represented by individuals. We define the species richness in fjord  $f$  at time (year)  $t$  as  $S_{f,t}$ , and the species settlement potential as  $R_{0,f}$ . A model in which  $S_{f,t}$ ,  $R_{0,f}$  is defined such as to account for the food web-dependent community buildup together with intrinsically and extrinsically determined components of per-species settlement,  $R_f(\bullet)$ , and per-species persistence,  $P_f(\bullet)$ , is given by

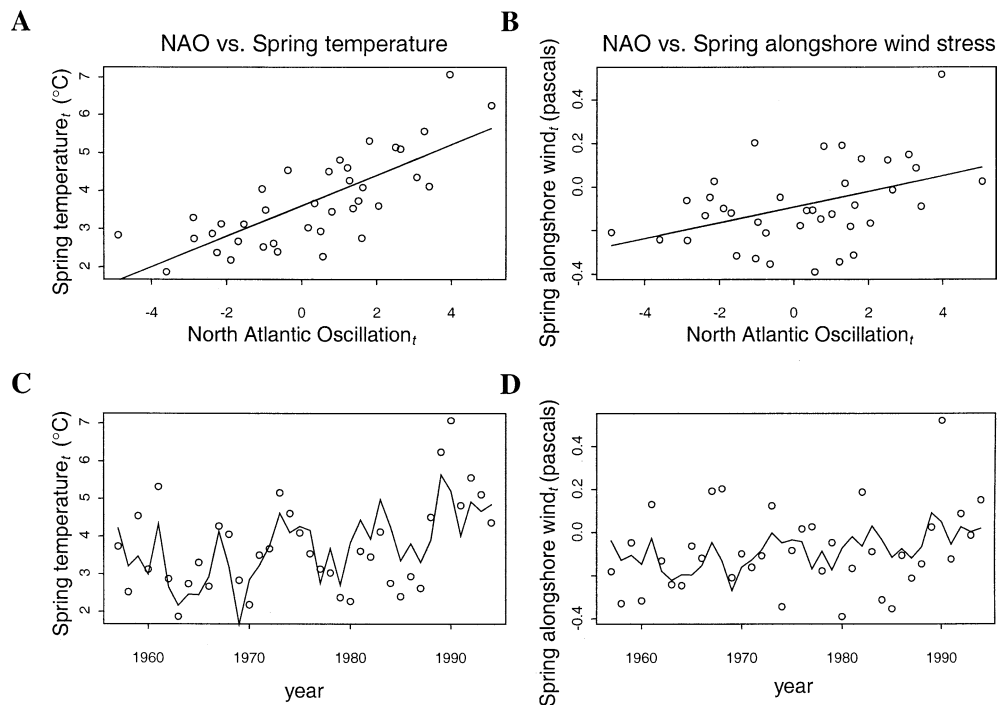
$$S_{f,t} = S_{f,t-1} R_{0,f} R_f(\bullet) P_f(\bullet) \quad (1)$$

Very little can be assumed about the shape of the functions  $R(\bullet)$  and  $P(\bullet)$ . By analogy to population dynamics (Royama 1992; Turchin 1995), we used exponential functions to describe these relationships to accommodate for the fact that adding one species to a community with few species will have a more profound effect than adding one species to a community with many species (Lekve et al., unpublished). The settlement rate,  $R_f(\bullet)$ , and persistence rate,  $P_f(\bullet)$ , may thus (except for a constant, which is absorbed into the  $R_0$  component) be expressed as

$$R_f(\bullet) = \exp\{-\alpha_f s_{f,t-1} + \underline{\kappa}_f^T \underline{w}_t\} \quad (2)$$

and

**Fig. 5.** Relationship between environmental covariates 1957–1994: NAO versus spring temperature (**A**) and NAO versus spring alongshore wind stress (**B**); linear fit of temperature and wind stress as a function of NAO (raw data, *open circles*; fitted values, *lines*); temperature =  $3.60 + 0.40$  NAO (**C**); wind =  $-0.09 + 0.04$  NAO (**D**)



$$P_f(\bullet) = \exp\left\{-\beta_f s_{f,t-1} - \gamma_f^T \underline{w}_t\right\} \quad (3)$$

where  $\underline{w}_t$  is a column vector containing the environmental variables, and the vectors  $\underline{\kappa}_f^T$  and  $\underline{\gamma}_f^T$  represent the coefficients of the extrinsic effects on the rates of settlement and persistence, respectively. Furthermore,  $s_{f,t} = \ln(S_{f,t} + 1)$  is included on the log scale. The parameters  $\alpha_f$  and  $\beta_f$  reflect the effect of species richness (cf. Brown et al. 2001) on settlement and persistence. Substituting Eq. 2 and Eq. 3 into Eq. 1 yields:

$$S_{f,t} = S_{f,t-1} R_{0,f} \exp\left\{-\left(\alpha_f + \beta_f\right) s_{f,t-1} + \left(\underline{\kappa}_f^T - \underline{\gamma}_f^T\right) \underline{w}_t\right\} \quad (4)$$

Notice the multiplicative nature of the model. The settlement rate can reasonably be seen as a multiplicative function of species number already present when considering how the succession process works: certain species are opportunists and must be present before other species can utilize the resources of the community. Thus, when there are few species, the overall effective settlement rate will be low because a suitable combination of prey or competitors might not yet be present.

Ideally, the recruitment and persistence equations should be fitted separately. However, no data on immigration and persistence rates are available for the Skagerrak coast. As we have species number data, we can only determine  $\alpha_f + \beta_f = a_f$  and  $\underline{\kappa}_f^T - \underline{\gamma}_f^T = \underline{b}_f^T$ , yielding:

$$S_{f,t} = S_{f,t-1} R_{0,f} \exp\left\{-a_f s_{f,t-1} + \underline{b}_f^T \underline{w}_t\right\} \quad (5)$$

An order-one process is indeed found appropriate for our data, which suggests that delayed feedback loops may properly be seen as negligible (at the community level) in this system.

Determining the parameters of the model

The negative log likelihoods of the Poisson distribution (McCullagh and Nelder 1989) for the derived model of the

number of fish species were minimized by the S-plus routine “nlminb” (Venables and Ripley 1997) for each of the fjords independently. Different combinations of wind and temperature at time  $t$  and NAO at time  $t$  and  $t - 1$  entered the models as environmental forcing variables. Among biologically appropriate models, the Corrected Akaike Information Criterion (AIC<sub>C</sub>; Brockwell and Davies 1991) was applied for model selection (Table 2).

This rather simple model of the community processes of fish in the coastal zone is able to capture important features of the dynamics of species richness in the fjords/areas studied along the Norwegian Skagerrak coast (Fig. 6). For several of the fjords, the model estimates closely follows the observed number of species (see areas SO, KR, GE, GI, and TJ in Fig. 6; acceptable  $R^2$  values; see Table 2). The following oceanographic and biological features may be important to understand why some of the fjords/areas are well described by the foregoing model, while further modeling effort is required to describe the dynamics of the other fjords/areas.

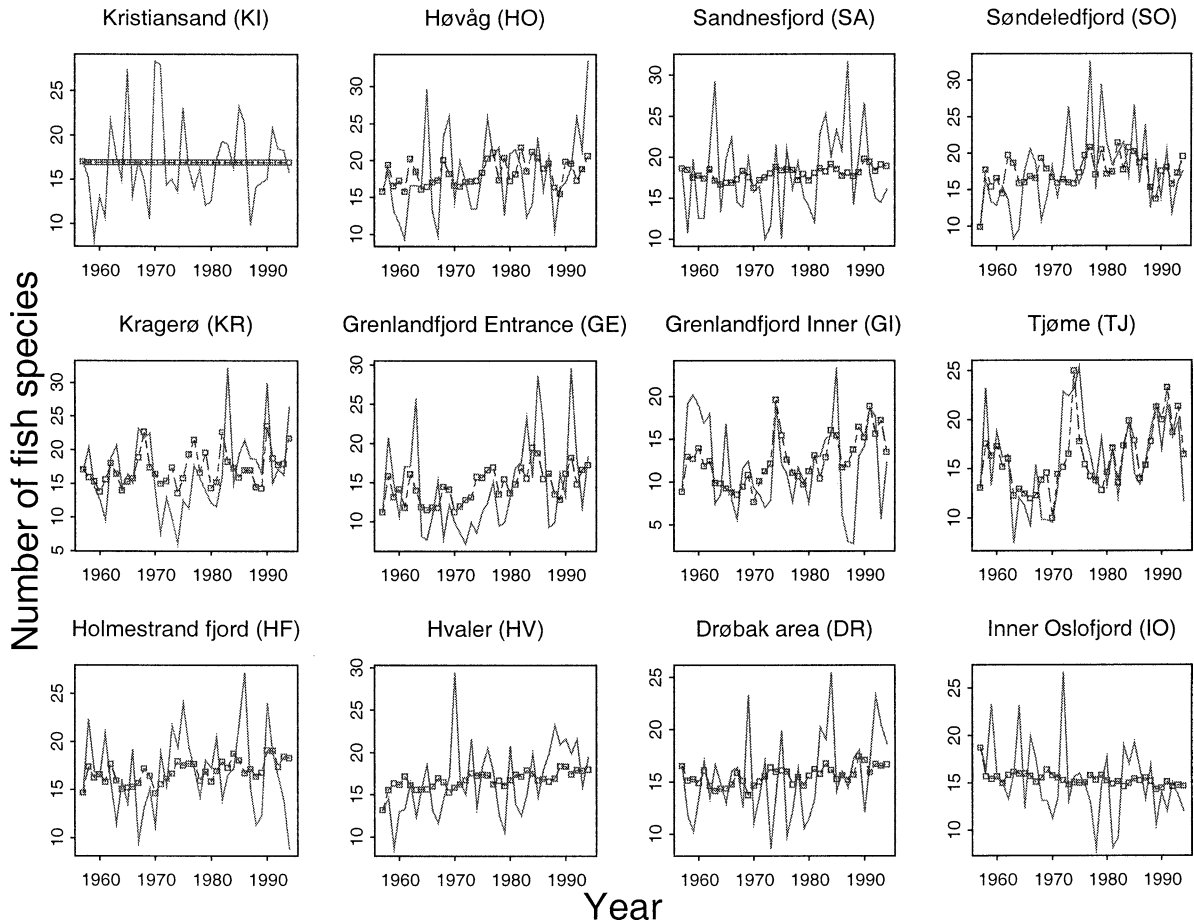
It has earlier been observed that the Oslofjord area displayed a different temporal pattern of species richness than the rest of the area (Lekve et al. 1999). Notably, this applies to the inner fjord and the outer east side (Hvaler, Drøbak, Inner Oslofjord in Fig. 1). This result was rather surprising, as there is a very shallow sill of only 19 m at Drøbak (Fig. 1), whereas the divergent patterns were observed both inside and outside this sill. The results from the model described by Eq. 5 may provide some explanations to this observation: in none of the models for the Oslofjord area stations (Hvaler, Drøbak, Inner Oslofjord) are wind and temperature selected (within the limits set by the AIC<sub>C</sub> criterion) as environmental variables (Fig. 7). Noting that wind is a proxy measure, we believe that the large-scale processes responsible for this spatial difference can be attributed to the influence of the main current in the Skagerrak area, the Norwegian Coastal Current (NCC; Danielssen et al. 1996, 1997; cf. Fig. 1). As this current flows around the coast, it plays a homogenizing role in the fjords exposed to its water

**Table 2.** Environmental forcing variables entering models of fish species richness fitted separately for 12 fjords/areas along the Norwegian Skagerrak coast

	Forcing at time $t$	Forcing at time $t - 1$	$R^2$
KI: Kristiansand (Topdalsfjord)	–	–	–0.00
HO: Høvåg (Steindalsfjord)	<i>Wind<sub>t</sub>, Temp<sub>t</sub></i>	<i>NAO<sub>t-1</sub></i>	0.10
SA: Sandnesfjord, Risør	–	<i>NAO<sub>t-1</sub></i>	0.03
SO: Søndeledfjord, Risør	<i>Wind<sub>t</sub>, Temp<sub>t</sub></i>	<i>NAO<sub>t-1</sub></i>	0.19
KR: Kragerø area	<i>Wind<sub>t</sub>, Temp<sub>t</sub></i>	<i>NAO<sub>t-1</sub></i>	0.27
GE: Grenlandfjord Entrance	<i>Temp<sub>t</sub></i>	<i>NAO<sub>t-1</sub></i>	0.24
GI: Grenlandfjord Inner	<i>Wind<sub>t</sub>, Temp<sub>t</sub></i>	<i>NAO<sub>t-1</sub></i>	0.18
TJ: Tjøme	<i>Wind<sub>t</sub>, Temp<sub>t</sub></i>	<i>NAO<sub>t-1</sub></i>	0.50
HF: Holmestrand fjord	<i>Temp<sub>t</sub></i>	<i>NAO<sub>t-1</sub></i>	0.08
HV: Hvaler	<i>NAO<sub>t</sub></i>	–	0.08
DR: Drøbak area	<i>NAO<sub>t</sub></i>	–	0.06
IO: Inner Oslofjord	<i>NAO<sub>t</sub></i>	–	0.04

Variables were selected within the limits set by the selection tool AIC<sub>C</sub> (Corrected Akaike Information Criterion; Brockwell and Davies 1991) and  $R^2$  values (Sen and Srivastava 1990) for the fit of the model

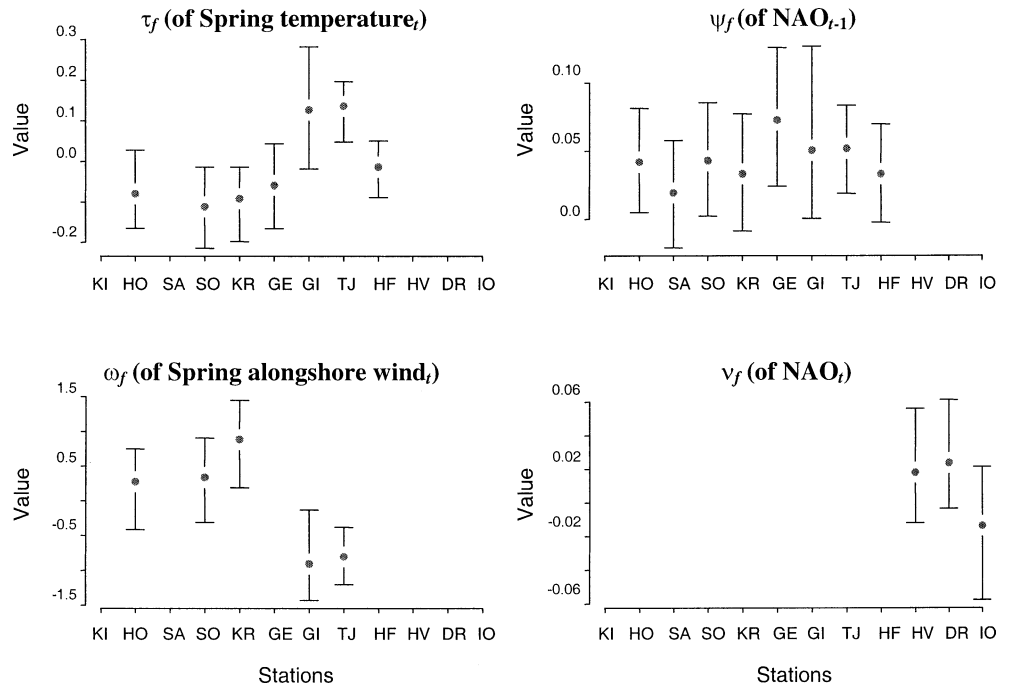
Source: Adopted from Lekve et al. (unpublished)



**Fig. 6.** Model predictions of fish species richness regulation of fjords along the Norwegian Skagerrak coast (cf. Fig. 1). Displayed are the observed number of species (e.g., estimated from repeated sampling of

four stations; Lekve 2001; *solid line*) and the one-step prediction of the model using only the environmental data as forcing variables (see main text; *stippled line with boxes*; Lekve et al., unpublished)

**Fig. 7.** Estimated parameter values for the coefficients of spring temperature at time  $t$  ( $\tau$ ), of the NAO at time  $t - 1$  ( $\Psi$ ), of spring alongshore wind at time  $t$  ( $\omega$ ), and of the NAO at time  $t$  ( $\nu$ ). The *error bands* are found from resampling of the residuals of the model and reoptimization 100 times. The inclusion of environmental terms in the models is based on biological selection within the limits set by the Corrected Aikake Information Criterion ( $AIC_C$ ) (Brockwell and Davies 1991)



masses as wind-driven currents create advective transport of, among other things, zooplankton into the fjords. The innermost stations of the Oslofjord (Drøbak, Inner Oslofjord) and the Hvaler area (possibly due to freshwater runoff from the largest river in Norway, Glomma) seem not to be influenced by advection from the NCC. Applying a different methodology, this overall assessment of a large-scale oceanic influence is confirmed in previous studies (Lekve 2001; Lekve et al. 2002c).

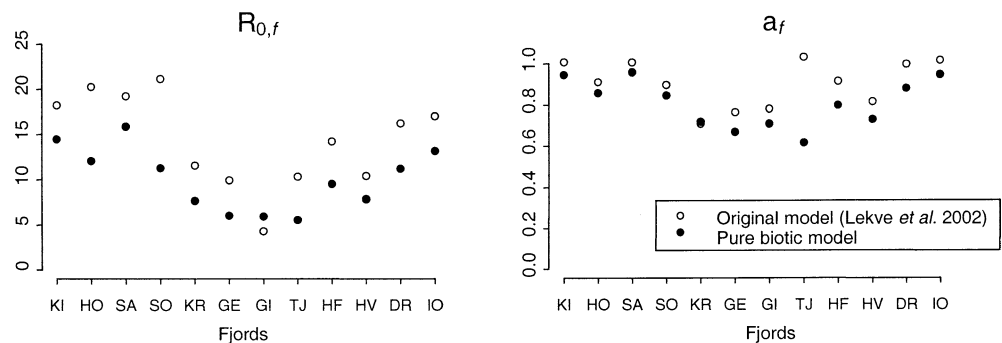
Our results are consistent with a hypothesis of strong influence from the Norwegian Coastal Current. Under such a hypothesis, we expect areas close to the open Skagerrak to be influenced by a similar set of environmental variables and to display similar intrinsic dynamics. Only the Greenland Inner and Kristiansand areas do not conform to a model of dynamics influenced by the NCC. The Greenland Inner is believed to be rather isolated. Thus, we should expect specific local processes to be important. Somewhat surprisingly, our results indicate that the Greenland Inner is influenced by much the same processes as the other fjords along the Skagerrak coast (although the estimated carrying capacity of richness, the  $\hat{R}_{0,f}$ , is low in this strongly human-influenced area) (Johannessen and Dahl 1996). On the other hand, we would expect the Kristiansand area to be influenced by the same processes as the rest of the coast because this area seems to be exposed to basin water masses. However, no environmental variables enter the

model for this fjord. One conclusion from these results is that overall processes may be revealed for fish species regulation in the coastal zone, but that local processes still have a strong influence that cannot be ignored.

The results from the model outlined (Eq. 5) suggest that the diversity of fish species is influenced by the species richness (Fig. 8, Table 3; all  $a_f$ 's are clearly different from zero).

It must be remembered that the properties of the system that can be investigated by this model are mainly *aggregate variability* (see following; Micheli et al. 1999). Many subtle details and peculiarities of each species generate the overall variability modeled. To a certain extent, the way the species number,  $S$ , is estimated takes species abundance into consideration by “weighting” species occurrences in a location by nearby locations (see Lekve et al. 2002a for details). Furthermore, there is great variability in life histories of fish (e.g., some species, i.e., cod, spawn millions of eggs whereas others, i.e., gobies, spawn few eggs and protect their eggs). Thus, in reality a complex web of changes of interaction coefficients is absorbed into the “ $a_f$ ” parameter. However, when we consider regulation around some long-term average species richness, the important point is *changes* among species, and these differences in life history traits will then be averaged out. However, the differences in life histories may very well be reflected in the  $R_0$  parameter (equivalent to the niche space). During certain environmental circum-

**Fig. 8.** Estimated values of  $R_{0,f}$  and  $a_f$  as given by Lekve (2001) and as estimated from the simplified model in Eq. 9



**Table 3.** Estimated values of  $R_{0,f}$  and  $a_f$  as given by Lekve (2001)

	Original model (Lekve 2001)		Pure biotic model (this paper)		BUGS model (this paper)	
	$R_0$	$a$ (AR-coeff)	$R_0$	$a$ (AR-coeff)	$R_0$	$a$ (AR-coeff)
KI	18.2 (11.9, 82.7)	1.007 (0.83, 1.49)	14.4	0.946	17.4	0.875
HO	20.3 (10.9, 73.0)	0.911 (0.70, 1.32)	12.0	0.857	21.5	0.946
SA	19.3 (11.3, 76.1)	1.007 (0.80, 1.43)	15.9	0.958	25.0	0.991
SO	21.1 (7.9, 73.4)	0.896 (0.60, 1.28)	11.3	0.846	15.9	0.872
KR	11.6 (6.3, 35.2)	0.708 (0.44, 1.03)	7.7	0.718	8.0	0.644
GE	9.9 (4.8, 35.6)	0.764 (0.48, 1.12)	4.7	0.607	6.8	0.656
GI	4.3 (2.9, 12.4)	0.780 (0.64, 1.18)	6.0	0.710	5.7	0.662
TJ	10.3 (6.4, 31.4)	1.032 (0.88, 1.37)	5.5	0.615	8.3	0.653
HF	14.2 (5.7, 64.5)	0.895 (0.58, 1.37)	10.4	0.832	13.1	0.780
HV	10.4 (4.8, 39.0)	0.914 (0.53, 1.25)	7.8	0.729	12.7	0.754
DR	16.2 (8.9, 65.9)	0.995 (0.76, 1.45)	11.2	0.880	18.0	0.895
IO	17.0 (10.7, 64.1)	1.014 (0.82, 1.45)	13.1	0.945	20.6	1.039

As estimated from the simplified pure biotic model in Eq. 9 and as found by BUGS estimation of Eqs. 10a and 10b



stances, certain species will gain competitive (dis)advantages. Communities dominated by different species may then display differential response to environmental disturbance and also differential patterns of regulation, which may an important factor to consider in the future when trying to explain the spatial pattern observed along the coast.

### Assessing the validity of the basic structure of the model

Figure 6 provides an illustration of the ability of the model to explain the variability existing along the Norwegian Skagerrak coast. The model outlined earlier may also be reformulated as the difference between species richness in 2 following years. To simplify the argument, we ignore the fjord subscript:

$$S_t = S_{t-1}R_0 \exp(-as_{t-1} + \underline{b}^T \underline{w}_t) \quad (6)$$

By subtracting  $S_{t-1}$  from both sides and rearranging, we obtain

$$\begin{aligned} S_t - S_{t-1} &= S_{t-1}R_0 \exp\{-as_{t-1} + \underline{b}^T \underline{w}_t\} - S_{t-1} \\ &= S_{t-1} \left( R_0 \exp\{-as_{t-1} + \underline{b}^T \underline{w}_t\} - 1 \right) \end{aligned} \quad (7)$$

Because, in a relatively species-rich community such as ours,  $S_{t-1} + 1 \approx S_{t-1}$  we may further write:

$$\Delta S_t = S_t - S_{t-1} = S_{t-1} \left( R_0 S_{t-1}^{-a} e^{\underline{b}^T \underline{w}_t} - 1 \right) \quad (8)$$

By also ignoring the external environmental forcing of the biological system and rearranging somewhat, we write

$$\Delta S_t = R_0 S_{t-1}^{(1-a)} - S_{t-1} \quad (9)$$

This model (the ‘‘pure biotic model’’) has been fitted to our data (fjord-by-fjord) using the ‘‘nls’’ routine in S-plus for nonlinear optimization (Venables and Ripley 1997). The parameters for  $R_0$  and  $a$  found by the complete model (Lekve 2001) are compared to those from this simplified model (see Fig. 8, Table 3). Observe that the estimates for both  $R_0$  and  $a$  are lower when environmental influence is excluded.

It is well known in population dynamics that a negative relationship exists between  $S_t$  and  $\Delta S_t$  that may cause artifacts in the density effects (Dennis and Taper 1994). By incorporating stochasticity both in the biological and in the observation process, we may appropriately check for such artifacts. Thus, to check for such artifacts a process model (Eq. 10a) and a sample model (Eq. 10b) were developed from Eq. 9 (ignoring the environmental covariates and incorporating noise):

$$s_t \sim N(\{1 - a\}^* s_{t-1} + \log R_0, \varepsilon_t^1) \quad (10a)$$

$$S_t \sim N(\exp\{s_t\}, \varepsilon_t^2) \quad (10b)$$

If the density effects found are due to statistical artifacts, a large proportion of the variance will be captured as noise in the observation process described in Eq. 10b. The coefficients of Eqs. 10a and 10b were estimated using BUGS (Spiegelhalter et al. 1999). As can be seen from Table 3, the density coefficient,  $a$ , changed only slightly, confirming that the richness-dependent regulation found here is real.

To compare the different ways of estimating the parameters, the data are plotted in Fig. 9. We have also fitted the models to our data using the environmental coefficients from the complete model (Lekve 2001) by using these values and covariates into Eq. 8; this is also displayed in Fig. 9. As can be seen, using the environmental covariates improves the fit of the model to the data. Furthermore, the influence of the environment does not change the biotic structure, providing strong support for the validity of our basic model.

The shape of the  $\Delta S$  function

In Fig. 9, the predicted shapes of the  $\Delta S$  function for each fjord are given. The  $\Delta S$  function may initially be an increasing function of  $S$  but always approaches some linear function for larger  $S$  values; this can be further explored by finding the derivative of the  $\Delta S$  function. From Fig. 10, the linearity of the high values of the  $\Delta S$  function is confirmed with the constant derivatives with (moderately) high  $S$  values. We see no flattening out as suggested by Brown et al. (2001).

Equilibrium number of species and the effect of climatic/environmental perturbations

Assuming that an equilibrium number of species exist, this can be found by setting  $S_t = S_{t-1} = S^*$  and fixing the environmental variables by using the estimated coefficients,  $\hat{\underline{b}}^T$  and the mean values of the variables,  $\bar{\underline{w}}$ . Starting with Eq. 6, we obtain

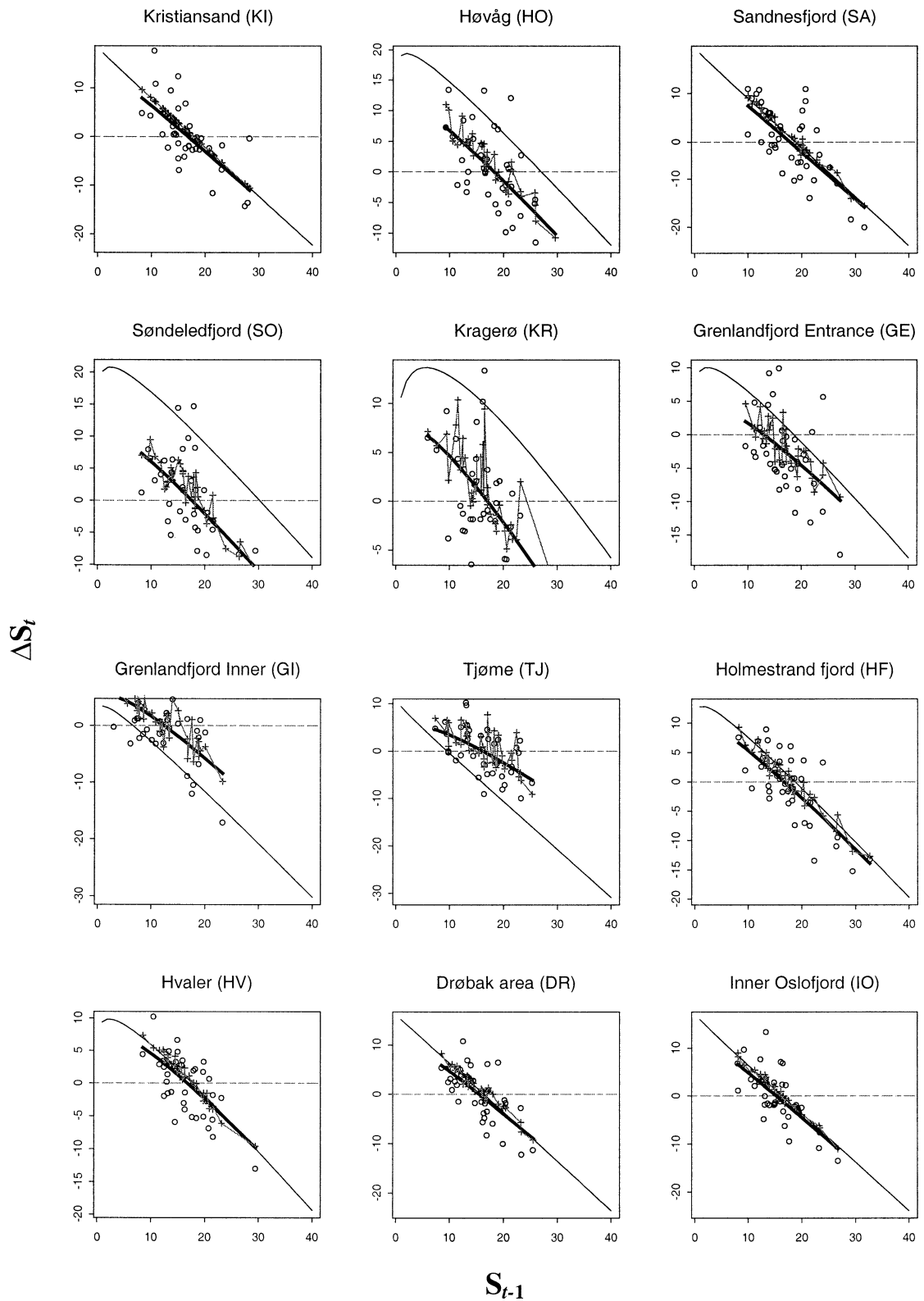
$$S^* = S^* R_0 \left\{ S^{*(1-a)} \exp\left(\hat{\underline{b}}^T \bar{\underline{w}}\right) \right\} \quad (11)$$

which may be rearranged as

$$S^* = \left\{ R_0 \exp\left(\hat{\underline{b}}^T \bar{\underline{w}}\right) \right\}^{1/a} \quad (12)$$

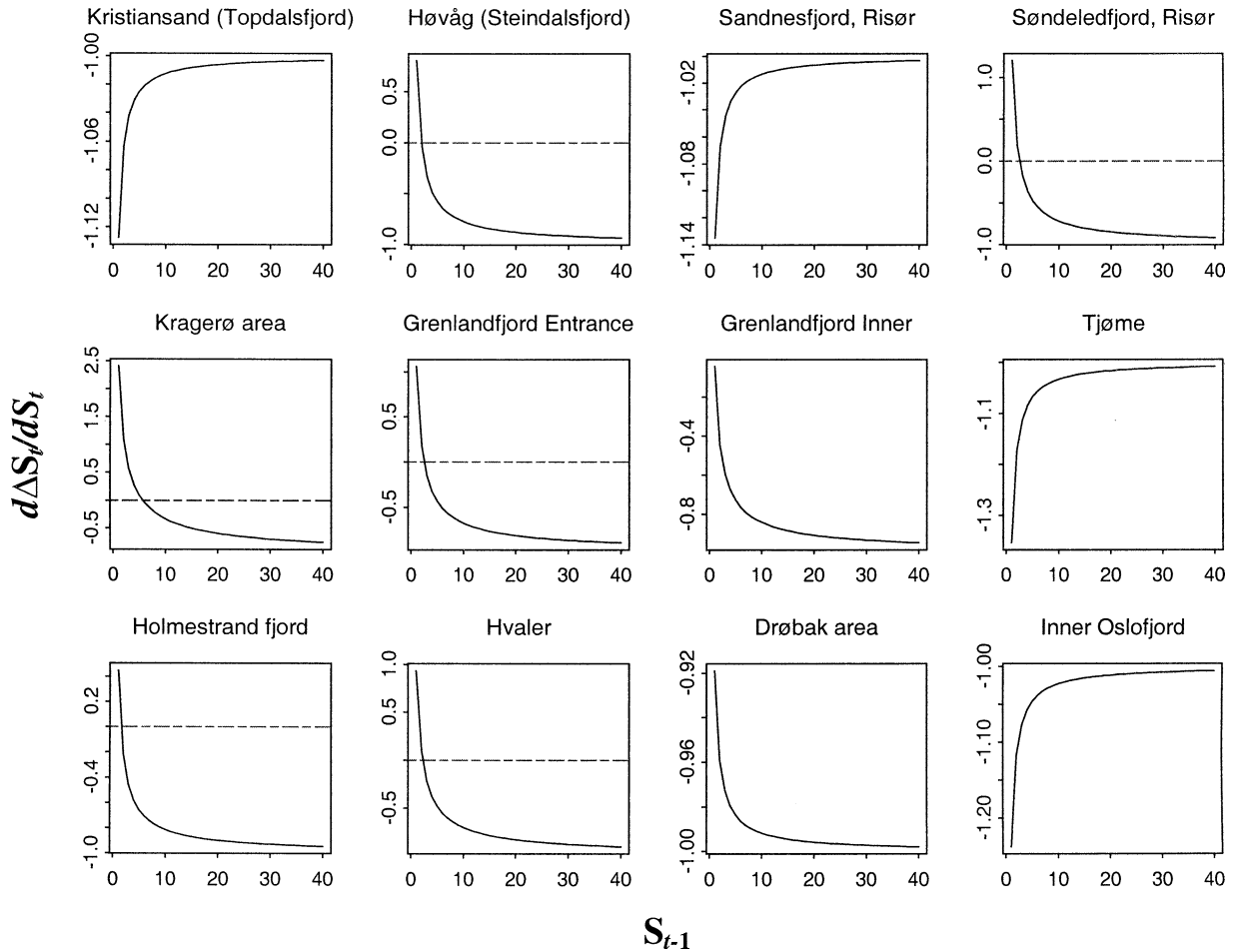
Using this expression for the equilibrium species number, we may ask how the number of species may change as the environment and overall climate change. We have chosen to explore this by taking two approaches, one considering the effect on species number assuming extreme values of the climatic covariates, and another considering the climatic covariates to be interrelated (see section on Climatic variables and Fig. 5), and then assuming what effect on species number will result given certain climatic scenarios.

Figure 11A shows the effect, for each fjord, when taking the first approach. Two phenomena should be



**Fig. 9.** Model of species richness regulation reformulated.  $\Delta S_t$  versus  $S_{t-1}$  (open circles). Thin smooth line, prediction from the pure biotic model of Eq. 9 using the estimates of  $R_{0f}$  and  $a_f$  found by Lekve (2001);

bold line, fit of the data using the pure biotic model in Eq. 9; jagged gray line with "+", fit of the pure biotic model to the data including the environmental covariates



**Fig. 10.** The shape of the derivative of the  $\Delta S$  function  $\left(\frac{d\Delta S_t}{dS_t} = R_0 S_{t-1}^{-a} - 1 - R_0 a S_{t-1}^{-a}\right)$ . For each fjord, the parameters obtained from the complete model are used to predict the complete shape of the function

noticed. First, environmental disturbance is seen to have the ability to create variability in the number of species in the model presented. Second, the equilibrium number of species will not change very much, remembering that the plotted extremes indeed may be considered as extremes.

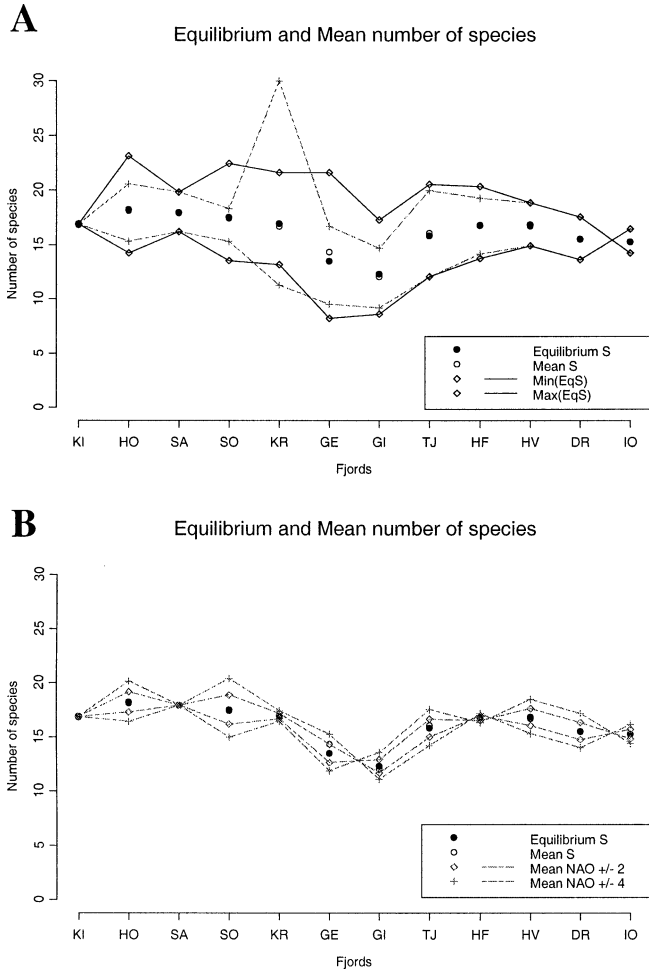
In Fig. 11B, we have then shown the effect of two climatic change scenarios, one for which the NAO changes by two (up and down) and one by which the NAO changes by four. As can be seen, the effect on the species number is only slight, the reason being that the various climatic factors counterbalance each other, a result that indeed seems very reasonable.

### Linking patterns and processes

Our model is a phenomenological model focusing on the species number per fjord directly. Although we do consider the observed species diversity as an emerging property of colonization and extinction, we might also like to derive the model from more basic processes, such as competition between species.

The dynamics within communities must necessarily be seen as resulting from the dynamics within each of the populations constituting the community. Micheli et al. (1999) recently made an attempt to describe this “dual nature of community variability.” Two types of community variability may be recognized: *compositional variability* (i.e., changes in the relative abundance of component species and species composition) and *aggregate variability* (i.e., changes in variables combining all species, such as total abundance or, as we have investigated, total species number). For the fish communities along the Skagerrak coast, the aggregate variability is high both for the number of species and for total abundance (Lekve et al. 1999). The abundance of several dominant species within the community also fluctuates dramatically (Fromentin et al. 1997, 1998; Bjørnstad et al. 1999a; Stenseth et al. 1999).

Hughes and Roughgarden (1998, 2000) have modeled the population dynamic processes as a system of generalized, density-dependent Lotka–Volterra competition equations in discrete time. They consider a community of  $S$  species (where the number of species,  $S$ , is considered to be fixed), and model the deviation of the population size of species  $i$  from its long-term average value (i.e.,  $n_{i,t} = N_{i,t} - \hat{N}_{i,t}$ ) by  $S$  equations:



**Fig. 11.** Equilibrium number of species [ $S^* = \{R_0 \exp(\underline{b}^T \underline{w})\}^{1/\alpha}$ ] and environmental perturbation. **A** Equilibrium number of species (filled circles) and mean number of species (open circles) and the perturbed equilibria of the number of species when all three environmental variables are set to its maximum and minimum (pluses with stippled lines) and when the NAO is set to its max/min value while the other two variables are set to their mean values (diamonds with solid line). **B** Equilibrium number of species (filled circles) and mean number of species (open circles) and the perturbed equilibria of the number of species when the values of the environmental variables are all expressed in terms of NAO equivalents. Diamonds and stippled lines,  $\pm 2$  NAO units, pluses,  $\pm 4$  NAO units

$$\begin{aligned}
 n_{1,t+1} &= (1 - r_1)n_{1,t} \\
 &\quad - r_1(\alpha_{12}n_{2,t} + \alpha_{13}n_{3,t} + \dots + \alpha_{1S}n_{S,t}) + z_{1,t} \\
 n_{2,t+1} &= (1 - r_2)n_{2,t} \\
 &\quad - r_2(\alpha_{21}n_{1,t} + \alpha_{23}n_{3,t} + \dots + \alpha_{2S}n_{S,t}) + z_{2,t} \\
 &\vdots \\
 n_{S,t+1} &= (1 - r_S)n_{S,t} \\
 &\quad - r_S(\alpha_{S1}n_{1,t} + \alpha_{S2}n_{2,t} + \dots + \alpha_{S(S-1)}n_{S-1,t}) + z_{S,t}
 \end{aligned}$$

(13)

where  $\alpha_{ij}$  is the interaction strength (the competition coefficient) of species  $j$  on species  $i$ ,  $r_i$  is the effective rate of increase of species  $i$ , and  $z_s$  is an independent identically distributed random variable with mean 0 and variance  $\sigma_z^2$ . Hughes and Roughgarden (1998, 2000) demonstrated how different systems of interactions between species (i.e., diffuse competition, limiting similarity, and random competition) create very different outcomes of community interactions in terms of biomass stability. They show how evenness in competitive ability between species promotes stability of the system and how strong interactions decrease the stability of systems.

The model of Hughes and Roughgarden (1998, 2000) represents a closed community without any immigration (and only implicitly extinction). To relax this assumption, we would need to consider the number of variables, the  $S$  number of equations, that enters into this model to be variable, increasing with successful settlement and decreasing with local extinction. Following the arguments of our own model, we would consider the settlement (i.e., increasing the number of equations) to depend upon the number of species (i.e., equations) already in the system. To develop and analyze such a model is not easy, but it is what might be needed to link the emerging ecosystem properties of species diversity with population dynamics processes.

Another avenue may be to adopt the approach of Stenseth and Maynard Smith (1984), working on an evolutionary time scale, and to formulate a more coarse model including both species number (as in our model) and the densities of the cooccurring species; that is,

$$S_t = S_{t-1} f(n_{1,t-1}, n_{2,t-1}, \dots, n_{S_{t-1},t-1}, S_{t-1}) \quad (14)$$

together with

$$\begin{aligned}
 \begin{bmatrix} n_{1,t} \\ n_{2,t} \\ \vdots \\ n_{S,t} \end{bmatrix} &= \begin{bmatrix} \alpha_{ij}(n_{1,t-1}, n_{2,t-1}, \dots, n_{S_{t-1},t-1}, S_{t-1}) \end{bmatrix} \\
 &\times \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \\ \vdots \\ n_{S,t-1} \end{bmatrix} + \begin{bmatrix} z_{1,t} \\ z_{2,t} \\ \vdots \\ z_{S,t} \end{bmatrix} \quad (15)
 \end{aligned}$$

where  $f()$  and  $\alpha_{ij}()$  are models describing the specific rates of change in species richness and deviations from the long-term average of the involved species, respectively; the matrix element  $\alpha_{ij}$  is defined for  $1 \leq i, j \leq S_{t-1}$ , where  $S_{t-1}$  is itself a dynamic variable. Using such an approach, the strength of the richness-dependent regulation will be a result of the deviations of the involved species from the carrying capacity for the species. Much work remains to develop the model and estimate the parameters of such matrix models. This set of models may provide a step toward unifying modeling of species dynamics and species richness, although the estimation of parameters

may be very complicated using real and complex biological models.

## Conclusion

Using an extensive data set on coastal fish communities from along the Norwegian Skagerrak coast as a basis, we have developed a community model describing the dynamics of species numbers at any given place and time, an enterprise closely related to an earlier study of Brown et al. (2001). By different modeling approaches we have investigated different aspects of the community dynamics of marine fish species. On this basis, we suggest that the rate of buildup of species numbers in a community will increase for communities being well under the equilibrium number, whereas this rate will, after a peak rate is reached, decrease toward a rate being proportional to the species number. That is, the more species there is in a community and the further it is away from the equilibrium (on the upper side), the higher turnover we would expect.

The deduced model is used for exploring the effect on the long-term species number of changing climate. We do suggest that the disturbance of the dynamics of the number of species is likely to be slight, due to the compensatory effect of various components of the climatically determined environment, suggesting that a high level of resilience is present in marine ecosystems.

The deduced model is nothing but a fragmentary contribution to the development of a (highly underdeveloped) theory for understanding and describing the community dynamics, a theory for which the species number necessarily must be a dynamic variable. In our effort, as described here, we have primarily focused on the dynamics of the species number. We do, however, suggest how the theory might be further developed so as to include the within-population dynamics together with a changing species number. We point out that such further development will encounter major challenges, challenges that necessarily must be solved if we are to understand the dynamics and maintenance of biodiversity.

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