

Abundance–distribution relationships and conservation of exploited marine fishes

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ABSTRACT: The effects of human exploitation on macroecological patterns have received little attention, although such investigations may highlight unique spatial and temporal changes characteristic of species and assemblages subject to persistent disturbance. In unexploited systems (mainly among temperate avifauna) positive relationships between local abundance and geographic distribution are prevalent for individual species through time (intraspecific pattern) and among species during fixed time periods (interspecific pattern). We investigated intraspecific and interspecific relationships for 24 common marine fishes on the Scotian Shelf and Bay of Fundy, Canada, some of which have been commercially exploited for several decades. Based on extensive fisheries-independent trawl survey data from 1970 to 2001, 16 of the 34 stocks, comprising 13 species, exhibited significant positive intraspecific relationships. Significant relationships were associated mainly with those stocks that demonstrated significant temporal trends in both abundance and geographic distribution. The time-averaged (32 yr) interspecific relationship was positive and significant at the largest scale examined. Significant annual interspecific relationships were also detected over 26 yr. Surprisingly, the slopes of the annual relationships increased systematically and doubled through time, probably due to size-selective exploitation, shifting target species, and associated species interactions. In contrast to previous studies, our results indicate that the contributions of individual species to the interspecific relationship can change through time, and these changes dramatically alter the interspecific abundance–distribution relationship. Temporal trends in the interspecific relationship have not previously been reported, and appear to be due to the large spatial- and temporal-scale effects of exploitation.

KEY WORDS: Exploited fisheries · Geographical range · Macroecology · Management · Marine protected area · MPA · Marine reserve · Range contraction · Scotian Shelf

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INTRODUCTION

Large-scale commercial fishing can be considered an uncontrolled experiment in nature that has produced serious biological, cultural and economic impacts (Johannes 1978, Hutchings & Myers 1994, Fogarty & Murawski 1998, Hall 1999, Kaiser & de Groot 2000, Pitcher 2001, Jackson et al. 2001, but see Johannes 2002). The recent appearance of degraded fisheries and ecosystems has led to the pursuit of alternatives to traditional

fisheries management practices with increasing interest in the application of marine protected areas (MPAs) (Agardi 1994, Shackell & Willison 1995, Allison et al. 1998, NRC 2000, Lubchenco et al. 2003). Under the assumption that mortality rates are reduced within such areas, an important and expected benefit is that organisms within the no-take boundaries will increase in abundance and eventually repopulate adjacent areas through larval dispersal and/or active movement (Carr & Reed 1993, Jennings 2000, McClanahan & Mangi

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2000). Consideration of design, establishment and monitoring criteria for MPAs continues (NRC 2000, Botsford et al. 2003, Hastings & Botsford 2003). The successful application of MPAs will probably be in those areas where the component species are well understood in terms of their dynamic geographical responses to changing abundance.

Concurrent with observations of fisheries declines and the promotion of marine conservation through designation of MPAs has been increased attention to macroecology, which reveals restricted statistical relationships through examination of ecologically relevant data at large spatial and temporal scales (Brown & Maurer 1989, Brown 1995). Of the many ecological characteristics examined, local abundance and geographical distribution have been shown to be interdependent for many taxa. Most frequently, species that have greater average local abundance show wider geographic distributions, generating positive correlations between these 2 variables (Hanski 1982, Brown 1984, Hanski et al. 1993, Lawton 1993, Gaston 1996). Correlation between these 2 variables occurs for multi-species comparisons of average values from similar taxa during time periods defined by the investigator (interspecific relationship) and for individual species' temporal patterns (intraspecific relationship) (reviewed by Gaston et al. 2000). These patterns seem somewhat intuitive, as at first glance they satisfy the presumption that more individuals require more space. However, it has been repeatedly demonstrated that the rate of increase in abundance exceeds that of geographic distribution, so that increases in abundance are not merely a function of expanding distribution (Gaston et al. 2000). The corollary (decreasing local abundance correlated with decreasing distribution) has received attention due to its implications for the conservation of relatively rare species with restricted distributions, as well as the increasing number of species undergoing abundance declines (Lawton 1993, Gaston 1999, Rodríguez 2002).

Most data and related analyses of abundance–distribution relationships come from temperate avifauna (Bock & Ricklefs 1983, Bock 1987, Brown & Maurer 1987, Gaston & Lawton 1990a, Gaston et al. 1998a,b, Rodríguez 2002). It has been suggested that examination of additional taxa, including marine (Gaston 1996) and freshwater (Gaston & Lawton 1990b) species may help assess the generality of abundance–distribution relationships. A recent assessment of findings revealed that interspecific patterns do extend to marine systems (Foggo et al. 2003). Additionally, since many marine species are actively exploited and some have been monitored for decades, marine data may provide empirical tests of patterns derived mainly from terrestrial studies (Frank & Leggett 1994).

The intraspecific abundance–distribution relationship has been examined and its existence confirmed in some commercially exploited marine fish species such as Atlantic herring, Atlantic cod and haddock (Winters & Wheeler 1985, Crecco & Overholtz 1990, MacCall 1990, Rose & Leggett 1991, Swain & Wade 1993, Marshall & Frank 1994, Swain & Sinclair 1994, Hutchings 1996, Overholtz 2002). One recognized consequence of the intraspecific relationship for fisheries is that if stock distribution declines with decreasing total abundance, the result is proportionally higher catch rates for a given level of fishing effort due to the non-random searching behavior of fishers (Paloheimo & Dickie 1964, Harley et al. 2001). Not only does such behavior make the use of catch rates from fisheries relatively insensitive to actual changes in population abundance; it also renders stocks susceptible to sudden collapse. Walters & Maguire (1996) reviewed the danger of using catch-rate indices in assessment models and suggested that ignoring this characteristic contributed to the demise of the largest stock of Atlantic cod in the western Atlantic—the northern cod.

Once established, intraspecific and interspecific patterns can form a basis for conservation practices (Lawton 1993, Gaston 1999, Rodríguez 2002). For example, a strong positive intraspecific correlation between local abundance and distribution provides a testable hypothesis of species recovery and export following the implementation of MPAs (Jennings 2000, Fisher & Frank 2002).

This paper reports the form and magnitude of abundance–distribution relationships of common commercial and non-commercial species on the Scotian Shelf, and evaluates the prevalence of intraspecific relationships. Interspecific relationships are also evaluated to address whether assemblages of common fish species conform to the positive, time-invariant relationship reported in other taxa where interspecific differences remained greater than the range of year-to-year variations in individual species abundance (Blackburn et al. 1998). Our expectation was that such a time-invariant relationship would not exist because exploitation effects may change the relative positions of species in interspecific comparisons. If true, the use of this relationship as a possible indicator of temporal community change would be warranted.

MATERIALS AND METHODS

Survey data. A fishery-independent groundfish trawl survey of the Scotian Shelf and Bay of Fundy has been conducted annually during July since 1970 by the Canadian Department of Fisheries and Oceans (NAFO Divisions 4V,W and X: Fig. 1). The survey follows a

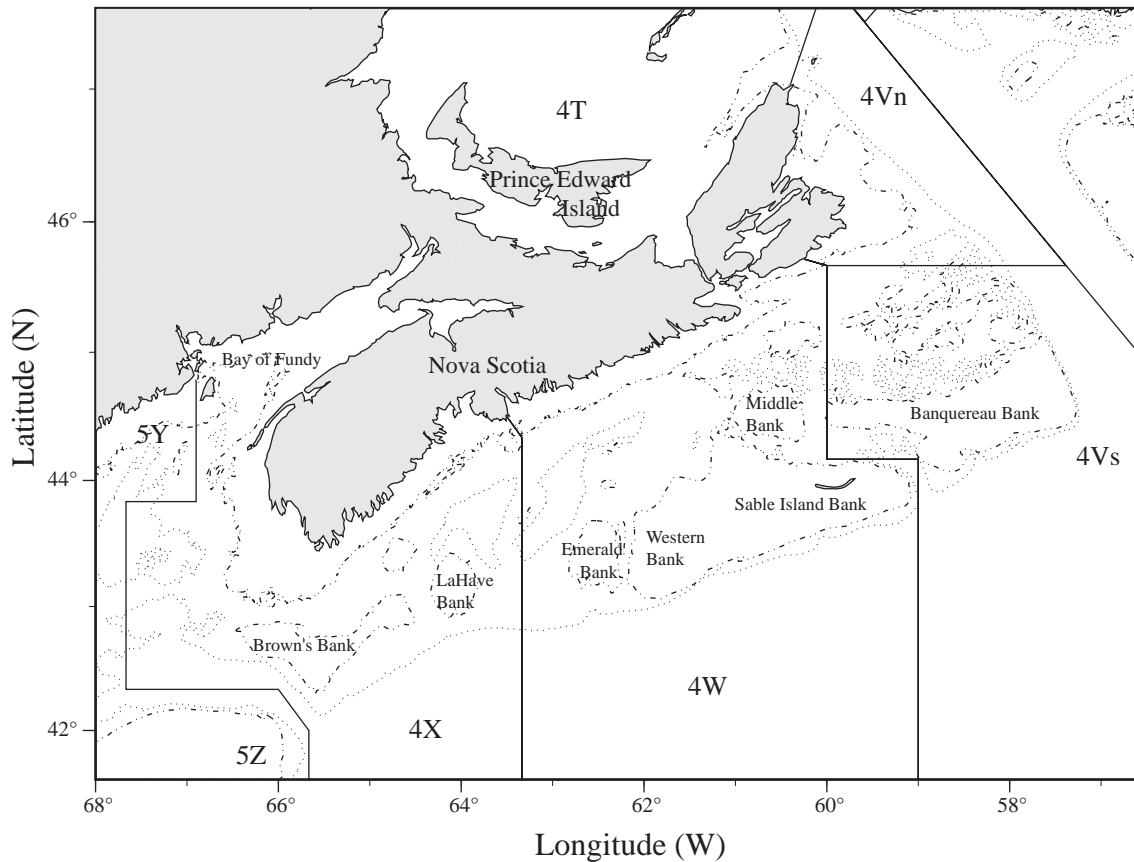


Fig. 1. Scotian Shelf and Bay of Fundy. Continuous lines: North Atlantic Fisheries Organization (NAFO) statistical divisions (some Scotian Shelf banks are labeled; July groundfish survey covered Divisions 4V,W and X to limits of continental shelf); dashed and dotted lines: 100 m and 200 m depth contours, respectively

standardized sampling protocol using a Western IIA otter trawl (wing spread 41 feet) with a 19 mm codend mesh lining towed for 30 min over a distance of approximately 3.25 km. Tow locations are assigned according to a random sampling design, with areas stratified by depth in order to provide unbiased estimates of population abundance through time (Doubleday 1981). Catch rates are standardized by tow distance and expressed as average number per tow per stratum or strata groupings. The primary objective of this survey has been to determine the distribution and abundance of exploited species. Secondly, this survey is conducted to gain information on non-target species (Doubleday 1981) and all species are recorded together with geospatial information on tow locations. Since the initiation of this survey, 5322 tows have been completed up to the year 2001, with an average of 166 tows per year (range 110 to 213). Data from this survey are presented at 2 spatial scales—at the species-specific management unit scale containing a given stock, as well as at the scale of the entire survey area for a group of common species (see later subsections).

Species and variables. We used occurrence (number of tows in which the species was present) throughout the entire history of the July survey to determine whether a species was included in the analyses. Since the ranked percentage of total survey tows occupied by each species declined exponentially from a maximum of 71%, with most of the 140 total species found in <1% of the tows (data from Table 1 in Shackell & Frank 2003), we limited the species examined to only those found in >10% of the tows. Below this cut-off point, annual as well as average estimates of distribution over the entire survey history were probably underestimated. Species with relatively low local abundance may be unrecorded from samples either because they are truly not there or because the sampling intensity is not sufficient to discover even 1 of them (McArdle 1990, Green & Young 1993, Hanski et al. 1993). Therefore, only species with high local densities were likely to have been detected at most locations at which they occurred, and only these species provided suitable geographical distribution estimates over the survey area.

Also, the species captured in >10% of survey tows represented those found at the most typical depths surveyed (i.e. on the continental shelf). Including additional species that occupied fewer tows would have included species found in habitats different from the majority of the surveyed area (e.g. longfin hake *Urophycis chesteri* in the abyssal slope habitat, see Simon & Comeau 1994). Inclusion of species predominantly from atypical habitats compared to the majority of the surveyed area is known to degrade interspecific relationships between abundance and distribution (Gaston & Lawton 1990a). Given these considerations, 24 fish species were included (see Table 1).

In order to avoid a potential positive bias in calculating the correlation between abundance and distribution that may result from the inclusion of zero values (Lacy & Bock 1986), we used only those tows in which the species was detected to calculate local abundance. Distribution was quantified as the minimum number of 10 min geographic squares (i.e. a grid system) that contained >90% of species abundance in each year. A very similar index of distribution (without use of a geographic-square grid system) has been demonstrated to suitably reflect actual distribution that depends only on spatial spread and not on overall species abundance (Swain & Sinclair 1994). Distributions are presented as proportions of the total number of grid squares surveyed annually at the stock or survey-wide scale for intraspecific and interspecific patterns, respectively. Proportions of surveyed areas were used instead of calculated absolute distributions to account for between-year differences in the intensity of sampling. All proportions were arcsine square-root-transformed prior to the analyses to correct for the known deviation of proportions from normal distributions (Zar 1984). Following the completion of the intraspecific analyses (described in next subsection), we have since confirmed that this metric of distribution is significantly correlated with the proportion of occupied tows for each stock across years, which remains an alternative metric of estimating geographical distribution (correlation between 90% distribution and proportion occupied tows, $r \geq 0.95$ for 29 stocks, $r \geq 0.87$ for remaining 5 stocks).

Intraspecific analyses. Intraspecific abundance–distribution relationships were evaluated at the level of management units in order to evaluate whether there were different relationships among adjacent stocks of the same species. This contrasts with previous studies that have focused primarily on the species level. Intraspecific relationships therefore represent abundance and distribution for each stock through time in management units that range from a single area (e.g. the NAFO Division 4Vn Atlantic cod stock) to shelf-wide Divisions 4V, W and X stocks (Fig. 1). The 24 species considered were classified as 34 stocks (see Table 1).

Of these stocks, 26 have been commercially fished; 5 additional non-commercial species were classified as single populations or split into Divisions 4V and W or Division 4X stocks based on the discreteness of their distributions throughout the majority of the survey years (Simon & Comeau 1994) (see Table 1).

Previous examination of intraspecific relationships demonstrated inconsistent support for the hypothesis that species showing wide variation in abundance or distribution are more likely to exhibit stronger intraspecific relationships (Gaston & Curnutt 1998, Gaston et al. 1998a). However, it is still hypothesized that a narrow range of variation in these measures may, in part, contribute to the lack of significant intraspecific relationships (Gaston et al. 2000). Gaston et al. (2000) reviewed studies displaying temporal trends in abundance and occupancy and found that they were associated with the strongest intraspecific relationships. Considering these previous findings, the coefficient of variation (CV) from both distribution and abundance were calculated for each stock. Stocks were classified as either exhibiting a significant correlation between abundance and distribution (16 stocks), or no correlation (18 stocks) and CVs were compared between these 2 groups. Spearman's rank-correlation coefficients between time and both distribution and abundance were also determined in order to examine whether temporal correlation of one or both variables was associated with the presence of the stock-specific intraspecific relationships.

Interspecific analyses. An interspecific abundance–distribution plot averaged over the survey period was constructed to test whether these variables were independent among species. While it was recognized that amalgamation of the data at the combined Divisions 4V, W and X scale would blur some of the stock differences specifically preserved for intraspecific analyses (see Table 1), we could not assume that stocks of the same species were independent data points when determining interspecific relationships. In addition to the average over the 32-yr history, annual interspecific relationships were also constructed using least-squares regression. The slopes of these annual relationships were examined to determine whether they conformed to the pattern of a study that described temporal change in the slopes of annual interspecific relationships as time-invariant (Blackburn et al. 1998).

RESULTS

Intraspecific relationships

Stock scale. Significant relationships between abundance and distribution were evident in 16 out of 34 stocks, which comprised more than half the species

Table 1. The 24 species in 34 stocks within management areas shown in Fig. 1. Code: 2-letter codes for species identification in interspecific plots (Figs. 3, 4 & 6). Years: number of years species was present in stock area; I.C.: Pearson correlation coefficients for intraspecific relationship of each stock. Correlation significance: * $p < 0.05$; ** $p < 0.01$

Management area	Species	Common name	Code	Years	I.C.
4V,W,X	<i>Squalus acanthias</i> ^a	Spiny dogfish	sd	32	0.33
	<i>Clupea harengus</i>	Atlantic herring	hr	32	0.73**
	<i>Argentina silus</i>	Argentine	ar	32	0.17
	<i>Lophius americanus</i>	Monkfish	mn	32	0.49**
	<i>Brosme brosme</i>	Cusk	cu	32	0.61**
	<i>Merluccius bilinearis</i> ^a	Silver hake	sh	32	0.53**
	<i>Pollachius virens</i> ^a	Pollock	pk	32	0.50**
	<i>Urophycis chuss</i> ^{b,c}	Red hake	rh	29	0.87**
	<i>Macrozoarces americanus</i> ^c	Ocean pout	pt	32	0.22
	<i>Anarhichas lupus</i>	Striped Atlantic wolffish	wl	32	-0.32
	<i>Glyptocephalus cynoglossus</i>	Witch flounder	wt	32	0.46**
<i>Hippoglossus hippoglossus</i> ^a	Halibut	hl	32	0.13	
4V,W	<i>Melanogrammus aeglefinus</i> ^a	Haddock	hd	32	0.65**
	<i>Urophycis tenuis</i> ^a	White hake	wh	32	-0.27
	<i>Hemitripterus americanus</i> ^{a,c}	Sea raven	sr	32	0.25
	<i>Myoxocephalus octodecemspinosus</i> ^c	Longhorn sculpin	ls	32	0.08
	<i>Triglops murrayi</i> ^c	Mailed sculpin	ms	31	0.38*
	<i>Hippoglossoides platessoides</i> ^a	American plaice	pl	32	0.33
	<i>Limanda ferruginea</i>	Yellowtail flounder	yf	32	0.34
<i>Pseudopleuronectes americanus</i>	Winter flounder	wf	32	0.35*	
4Vs,W	<i>Raja ocellata</i>	Winter skate	ws	32	-0.20
	<i>Raja radiata</i> ^a	Thorny skate	ts	32	0.71**
	<i>Raja senta</i> ^a	Smooth skate	ss	32	0.52**
	<i>Gadus morhua</i>	Atlantic cod	cd	32	0.78**
4X	<i>Gadus morhua</i>	Atlantic cod	cd	32	0.20
	<i>Melanogrammus aeglefinus</i> ^a	Haddock	hd	32	0.51**
	<i>Urophycis tenuis</i> ^a	White hake	wh	32	0.15
	<i>Hemitripterus americanus</i> ^{a,c}	Sea raven	sr	32	-0.21
	<i>Myoxocephalus octodecemspinosus</i> ^c	Longhorn sculpin	ls	32	0.25
	<i>Triglops murrayi</i> ^c	Mailed sculpin	ms	31	0.31
	<i>Hippoglossoides platessoides</i> ^a	American plaice	pl	32	-0.02
	<i>Limanda ferruginea</i>	Yellowtail flounder	yf	32	0.33
<i>Pseudopleuronectes americanus</i>	Winter flounder	wf	32	0.67**	
4Vn	<i>Gadus morhua</i>	Atlantic cod	cd	32	0.41*

^aSpecies currently considered 'highest priority candidates' by COSEWIC (2004) (see 'Discussion')

^bTwo sampling years (1977, 1978) excluded (outliers)

^cStocks identified by spatial distributions (see 'Materials and methods')

examined (Table 1). The ranked strengths of the intraspecific relationships were not correlated with the ranked species occurrences, so species encountered frequently over the entire survey history were not any more likely to exhibit significant abundance–distribution relationships than those collected in fewer samples. All the significant relationships were positive (Fig. 2a–e). Of the 24 species examined, 9 were composed of more than 1 stock, generally representing discrete stocks on the eastern and western Scotian Shelf. The majority did not show differences between areas (Table 1). Atlantic cod showed the greatest contrast between areas. The eastern Scotian Shelf stocks (especially the Divisions 4Vs and W stock) exhibited positive relationships between abundance and distribution

(Fig. 2e), while the stock on the western Scotian Shelf (Division 4X) showed no relationship (Fig. 2f).

The stocks that exhibited significant intraspecific relationships had an average CV of 0.20 for distribution (range 0.09 to 0.38), while the stocks that did not show intraspecific relationships had an average CV of 0.14 (range 0.04 to 0.27). For abundance, stocks that showed intraspecific relationships had an average CV of 0.27 (range 0.16 to 0.42), with a very similar average CV for those stocks that failed to show an intraspecific relationship (average 0.25, range 0.07 to 0.54). Therefore, high inter-annual variability in either distribution or abundance was not necessarily associated with significant abundance–distribution relationships (but compare cod stocks: Fig. 2e,f).

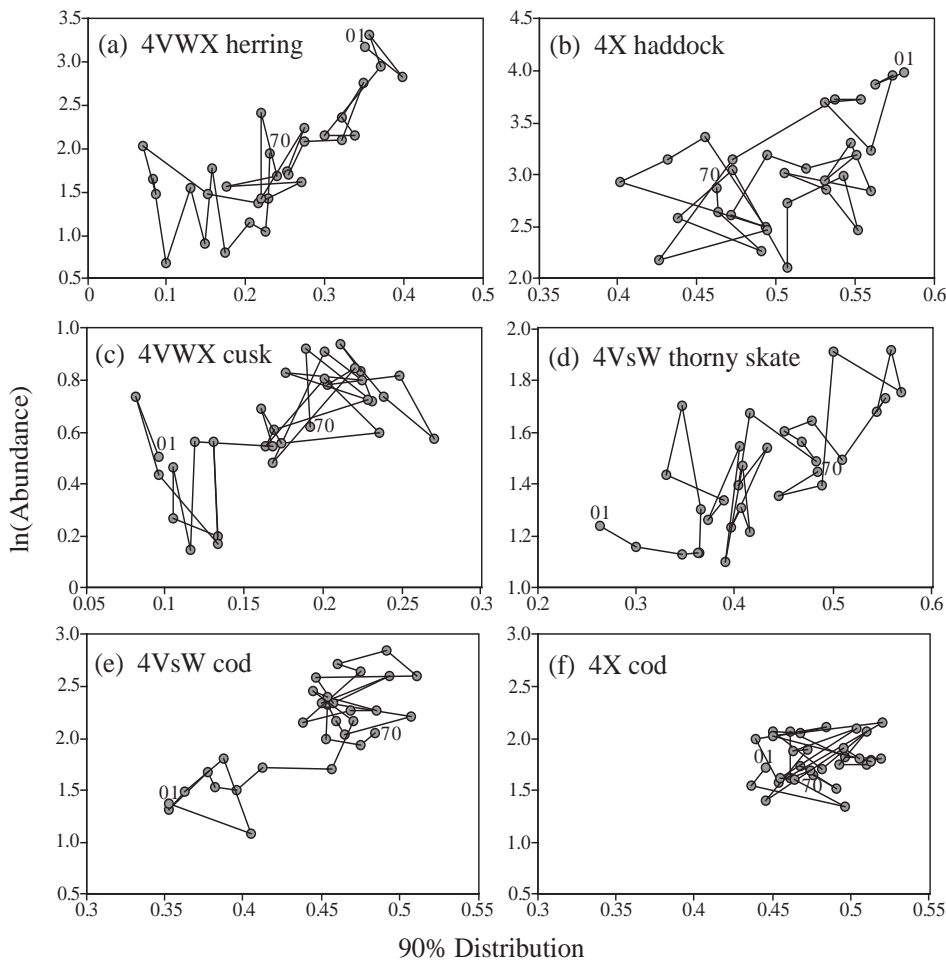


Fig. 2. Positive, significant intraspecific abundance–distribution relationships for (a,b) 2 stocks that exhibited significant positive temporal trends in abundance and/or distribution, and (c,d) for 2 stocks that underwent significant negative temporal trends in abundance and distribution. (e) Divisions 4Vs and W cod stock demonstrated a significant positive relationship having undergone declines in abundance and distribution; (f) Division 4X cod stock demonstrated no intraspecific relationship and underwent no significant temporal trends in either variable. 70, 01: sample years 1970 and 2001, respectively. All correlation statistics in Table 1, temporal trends in Fig. 3

Effects of temporal trends. Spearman's rank-correlation coefficients between abundance and time revealed that 18 out of 34 stocks exhibited significant temporal trends (Fig. 3). Of these temporal correlations, 13 were significantly positive, while 5 were significantly negative (Fig. 3: abscissa). Significant temporal trends for the minimum area containing 90% abundance occurred for 21 stocks, of which 14 and 7 stock-distribution trends were positive and negative, respectively (Fig. 3: ordinate). Significant trends in these 2 variables were not randomly associated among stocks. Of the 16 significant intraspecific relationships for the stocks (Fig. 3: based on data in Table 1), 10 stocks showed significant temporal correlation for both abundance and geographic distribution. Of the remaining 6 stocks, 3 showed significant abundance–distribution correlation without significant trends in either abundance or distribution (Fig. 3). Another 2 stocks (4X haddock and 4V and W haddock) showed significant positive temporal trends in abundance only, while 4V and W mailed sculpin exhibited only a significant positive temporal trend in distribution. Spiny

dogfish, striped Atlantic wolffish, 4V and W white hake, 4X longhorn sculpin, and 4X yellowtail flounder failed to demonstrate significant intraspecific trends despite exhibiting temporal increases in both abundance and distribution (Fig. 3). The observation that significant positive intraspecific abundance–distribution relationships were displayed by stocks demonstrating concomitant temporal increases (Fig. 2a,b) and decreases (Fig. 2c–e) indicated that intraspecific relationships were characteristic of populations displaying a range of trajectories.

Interspecific relationship

Scotian Shelf. The interspecific correlation was positive and statistically significant when average abundance and distribution were calculated for each species across the 32-yr survey period ($p = 0.012$, Fig. 4). This relationship demonstrated that among those species that were consistently captured, some were both narrowly distributed with low local abundance (e.g.

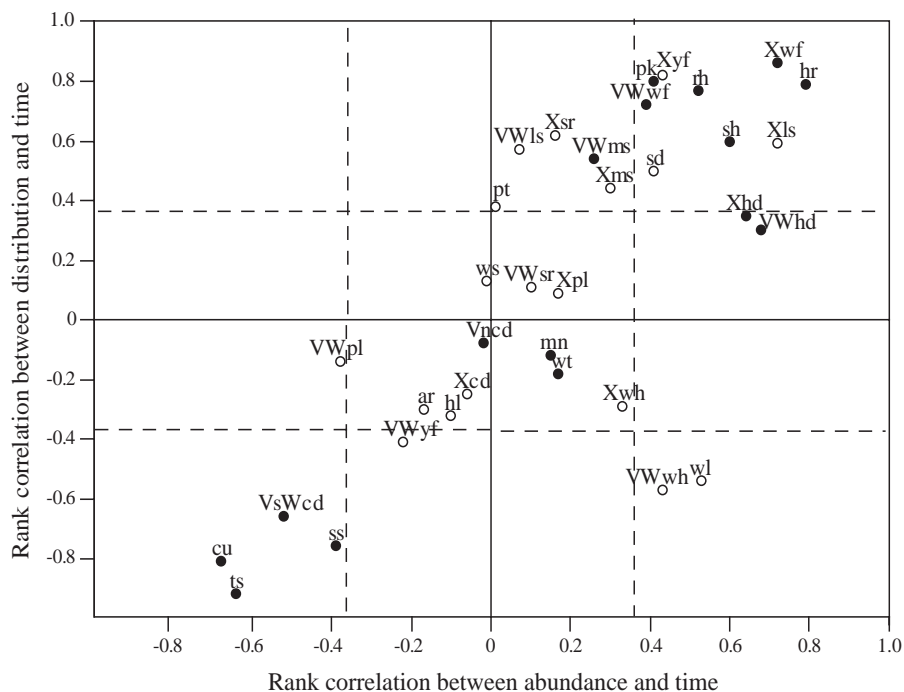


Fig. 3. Temporal Spearman's rank-correlation of abundance plotted against temporal Spearman's rank-correlation of distribution for the 34 stocks. Uppercase letters: multiple stocks of same species; (○) stocks with no intraspecific relationship; (●) stocks with significant positive intraspecific relationship (see Table 1 for stock listing and species codes); dashed lines: boundaries of significant ($p < 0.05$) temporal rank correlation

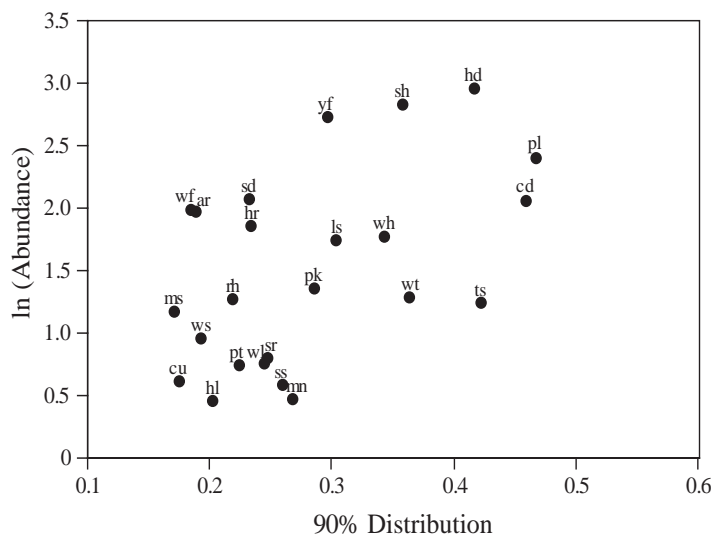


Fig. 4. Interspecific abundance–distribution relationship for 24 species from Scotian Shelf listed in Table 1, averaged over 32 yr survey period (1970 to 2001). Each data point can include more than one stock, species codes as in Table 1. Significant correlation between abundance and distribution is evident ($r = 0.50$, $n = 24$, $p = 0.012$)

cusks, halibut, winter skate). Others demonstrated concomitant wide distribution with higher local abundance (e.g. American plaice, Atlantic cod, haddock).

Temporal variability. All 32 annual interspecific abundance–distribution relationships had positive slopes, 26 of which were statistically significant. There were 2 interdependent temporal patterns apparent: the slopes of the relationship doubled over time (Fig. 5a) and the correlation between abundance and distribution in the annual relationships increased significantly (Fig. 5b). The overall temporal pattern of increasing interspecific slopes was not biased by our use of ordinary least-squares (OLS) regression. Reduced major axis regression (RMA) produced a very similar pattern (Spearman's rank-correlation coefficient between OLS and RMA annual regression slopes, $r_s = 0.795$, $p < 0.001$). It is possible that the widespread species became more abundant for a given level of distribution, thus accounting for the increase in slope. Alternatively, the species with restricted distributions could have shown decreases in

local abundance at a given low level of distribution, thereby depressing the minimum abundance values. These possible scenarios and potential mechanisms are outlined in Fig. 6a, while the actual differences between 1970 and 2001 demonstrated a combination of these factors with changes in many species across the continuum (Fig. 6b). The temporal trend of increasing slopes (Fig. 5a) was quite dramatic, and indicated that throughout the history of the survey, some of the underlying species changed their abundance and/or distribution to such a degree as to systematically alter the form of the interspecific pattern (Fig. 6b).

DISCUSSION

Intraspecific relationships were evident in nearly half the stocks examined, with the emergence of patterns having important implications for the establishment and evaluation of MPAs. The interspecific relationships we document support the proposition that such patterns may be general, although annual differences were evident and illustrate the effects of long-term ecological perturbation driving changes in the macroecological relationship.

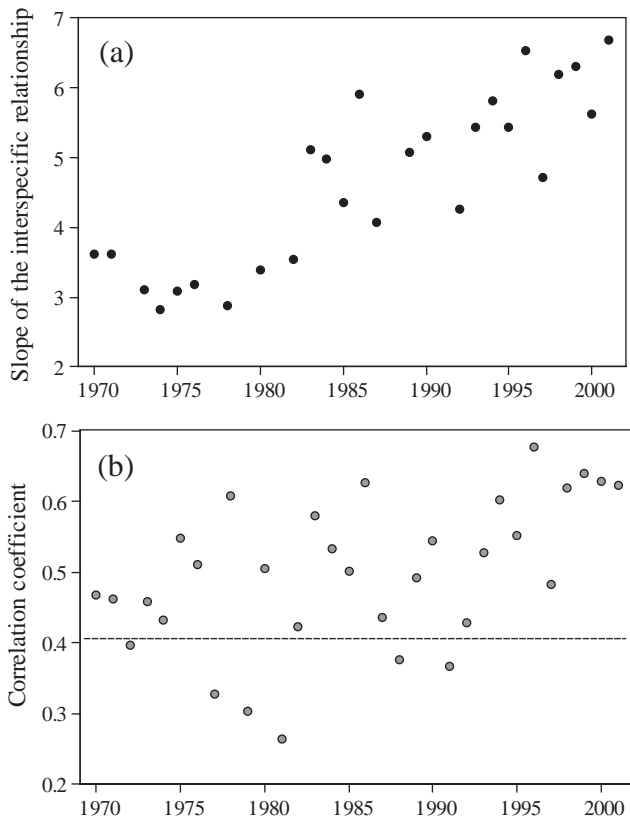


Fig. 5. (a) Temporal trend in slopes from least squares regression of 26 significant annual interspecific abundance–distribution relationships for Scotian Shelf data (Spearman's rank-correlation coefficient between slope and year $r_s = 0.85$, $n = 26$, $p < 0.001$). (b) Temporal trend in correlation coefficient for 32 annual interspecific abundance–distribution plots (Spearman's rank correlation coefficient $r_s = 0.52$, $n = 32$, $p < 0.01$); dashed line: minimum correlation for significant interspecific relationships ($p < 0.05$, 22 df)

Intraspecific relationships

Positive relationships between abundance and distribution at the management unit scale are important to recognize, especially for populations influenced by exploitation that can act directly on the target species and/or indirectly on other assemblage members. As in other systems, new fisheries have expanded on the Scotian Shelf to include additional species as many traditional stocks declined (Zwanenburg 2000). Also, many large, formerly abundant species have remained at low levels of abundance despite a steady reduction in fishing effort during the past decade (Fisher & Frank 2002). Therefore, it is advantageous to examine which of the abundant and widespread populations demonstrate relationships between abundance and distribution so that such population trajectories are incorporated into evaluations of stock status and in the siting of areas that require special consideration, e.g. MPAs.

Nearly half of the stocks examined exhibited significant positive relationships between local abundance and distribution (Table 1). These significant intraspecific relationships have a number of implications. First, stocks in decline may be at risk of 'double jeopardy' given that as local abundance decreases so too does distribution (Lawton 1993). This scenario has the potential to create the conditions for population extinction as both factors contribute independently to extinction risk (Rosenzweig 1995). Stocks in the current examination that clearly depicted double jeopardy included cusk (Fig. 2c), 4Vs and W smooth skate, 4Vs and W thorny skate (Fig. 2d), and 4Vs and W Atlantic cod (Fig. 2e), which all demonstrated precipitous declines in abundance and distribution. These species spanned the extremes of the assemblage abundance and distribution (Fig. 4) and emphasize that widespread species are also susceptible to this pattern of

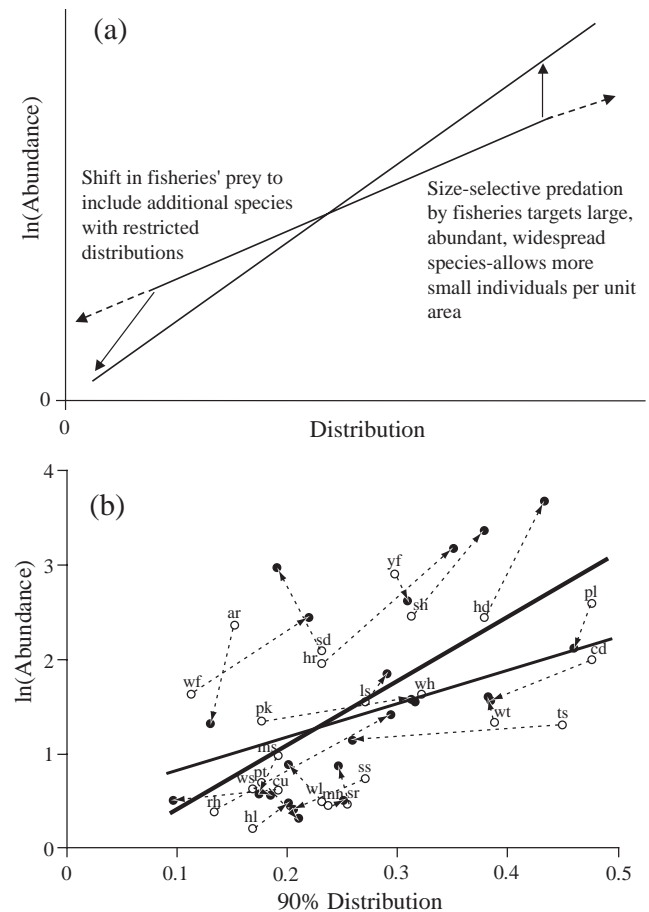


Fig. 6. (a) Schematic representation of 2 forces interacting to produce different interspecific abundance–distribution relationships based on same assemblage of species at different points in time. (b) Empirical relationships from Scotian Shelf using first and last years evaluated in this study; (○) and thin trend line: 1970; (●) and thicker trend line: 2001. Species codes as in Table 1; annual slopes from Fig. 5

decline. Recently, populations of cusk and Atlantic cod from areas including the Scotian Shelf were classified as 'threatened' and of 'special concern', respectively, by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2003). Of the 24 species examined in this study, 10 were recently additionally designated 'highest priority candidates' for future evaluation, as indicated in Table 1 (COSEWIC 2004).

Associated with the observation of concomitant decreases in abundance and distribution has been the hypothesis that, as a population declines, its spatial distribution declines due to loss of individuals towards distribution limits where population growth rates are low. Declines of this type are expected to leave the remaining population only in those areas in which the maximum intrinsic rate of population increase is maintained (Lawton 1993). This 'core area' idea is an important consideration for conservation. For example, such areas would be ideal locations for MPAs. Exploration of this prediction with bird species has reported equivocal support for the core-areas idea (Curnutt et al. 1996, Gaston & Curnutt 1998). However, Hutchings (1996) demonstrated the susceptibility of the widespread northern cod stock to decline from overfishing and his analysis indicated that high-density tows (>500 kg biomass) remained constant through time in the trawl surveys, while declines in all tows of lower density were occurring. These observations suggested that high-density areas were recruiting individuals from areas of lower density (Hutchings 1996), and supports Lawton's (1993) idea of core distributions for this stock. Examinations of this type should be included in fisheries management strategies because, if the core-area hypothesis is not supported for additional stocks, then stocks that decline in abundance may not end up in core areas but rather in demographic sink locations in which they are not able to successfully increase in abundance (Lawton 1993). Such a scenario would foreclose on a stock's ability to recover in the short-term despite any future level of spatial protection [but see Roberts (1998) for practical limits to source-sink analyses and alternate approaches used to designate protected areas]. Fogarty & Murawski (1998) (their Fig. 7) provided illustrations of the use of 10 min geographic squares to indicate historic spatial distribution of multiple species on Georges Bank in relation to contemporary fishery-closed areas. The use of these mapping techniques at various population sizes will provide data for managers on species-specific levels of protection from proposed MPA configurations.

The fact that both negative and positive temporal trends in distribution and/or abundance have been exhibited by these stocks (Fig. 3), underscores the fact that this relationship, best described by its double jeopardy potential as a population declines, can also

act as a double benefit for populations increasing in local abundance and distribution (Gaston 1999, Overholtz 2002). While increased abundance coupled with increasing distribution is clearly viewed as positive for some of these stocks (i.e. those of conservation concern), for other stocks, coupled changes in local abundance and distribution may confound fisheries management efforts directed at other species (e.g. recent Atlantic herring increases may inhibit recovery of Atlantic cod; Swain & Sinclair 2000). The fact that both negative and positive temporal trends were observed also suggests that changes in abundance and occurrence of species may be the result of changing trophic interactions. During ontogenesis, many of these species exist as both prey and predator with respect to other species in the assemblage, leading to complex interactions among species and life stages. The reduction of Atlantic cod abundance and distribution on the eastern Scotian Shelf, where it had historically been the dominant piscivore, may have allowed 1 or more of its prey or competitor species to increase in abundance and thereafter impact the recovery of Atlantic cod in the manner elucidated by Swain & Sinclair (2000), or otherwise. Recently, impacts of trophic interactions between formerly abundant large adult fishes, their juvenile offspring, and smaller fish species that fall prey to adult fishes (but compete with or prey on large-fish offspring) have been interpreted from simulations (Walters & Kitchell 2001). Their results suggest that unintended consequences for recovery may arise from single-species management and an ignorance of multi-species interactions.

In addition to demonstrating the susceptibility of numerous species to declines in abundance and distribution, a practical application of the significant positive relationships for increasing stocks is the intra-specific effect on stock recovery rates within MPAs. Covariation of abundance and distribution implies that with increases in abundance within MPAs, spatial expansion of the population will result in the spillover of individuals to the surrounding fished area, thereby adding to fishery yields but at the same time delaying the observed rate of recovery in the closed area (Jennings 2000). So, depending on the size of the protected area and species-specific rates of geographic expansion with increasing abundance (defined by the slope of the intraspecific abundance–distribution relationship), closed areas are expected to afford stock protection as an inverse function of the rate of transfer to the fished areas (Jennings 2000, Fisher & Frank 2002).

Despite assertion that intraspecific abundance–distribution relationships seem inevitable (Gaston et al. 1998a), previous examinations of possible intraspecific relationships provided evidence of both significant and non-significant relationships (Swain & Wade

1993, Marshall & Frank 1994, Gaston & Curnutt 1998, Gaston et al. 1998a,b, 1999). Examination of the range of abundance and distribution values, through comparison of CVs between stocks with significant and non-significant intraspecific relationships, showed no definite patterns. These findings largely support previous examinations which, at best, found inconsistent associations between variation in local abundance or distribution with the strength of intraspecific relationships (Gaston & Curnutt 1998, Gaston et al. 1998a).

In contrast to these findings, significant temporal trends in local abundance and distribution were associated with significant positive intraspecific relationships, as the majority of stocks that exhibited significant intraspecific relationships also displayed the strongest temporal trends in both variables (Fig. 3). These findings support results reported in other studies (Gaston & Curnutt 1998, Gaston et al. 1998a, 1999). Gaston et al. (1998a) proposed that strong temporal change in abundance may result in a temporal change in distribution due to local extinction following continued abundance declines, while oscillating (quickly recovering) changes in abundance would not result in changes in distribution due to time lags between declines in local abundance and local extinction. Thus, temporal trends in abundance appear to be necessary to cause trends in distribution, thereby setting up the conditions for particularly strong positive abundance–distribution relationships.

Interspecific relationships

The positive interspecific relationship demonstrated at the scale of the Scotian Shelf suggests that this fish assemblage conforms to the same general pattern generated by numerous other taxa at a variety of spatial scales (Hanski 1982, Brown 1984, Hanski et al. 1993, Lawton 1993, Gaston 1996). It is evident that at the assemblage level, species differed greatly in their average positions along the continuum from widespread and abundant to relatively restricted in distribution with low local abundance (Fig. 4). This pattern does not appear to be biased by phylogenetic relatedness, as members within the dominant families (Rajidae, Gadidae, Cottidae, Pleuronectidae) span both variables (Fig. 4). The interspecific pattern has ramifications for the census of marine biodiversity, in that although the survey coverage is quite extensive, additional intensive sampling is essential to unveil both the true spatial distribution and local abundance of additional species (Gaston 1999). Some other studies of large-scale marine biodiversity have circumvented the sampling intensity problem inherent in these surveys by using species lists or cumulative estimates of spe-

cies richness (Frank & Shackell 2001, Shackell & Frank 2003). While the use of species richness is useful in some instances, increased sampling effort and/or new techniques will be necessary to generate accurate species-abundance estimates and distributions for the majority of fish species that were not included in the analyses. Recognizing that these data were primarily collected to evaluate abundant, widespread, fished populations, if these surveys remain the only methods undertaken to sample regional biodiversity, complete knowledge of abundance or distribution for the majority of species will not be possible (Langton et al. 1995, Breeze et al. 2002, Shackell & Frank 2003).

In addition to the single averaged interspecific relationship (Fig. 4), the results of annual interspecific relationships may be among the first to show marked temporal trends in the slope of these relationships, since these almost doubled between 1970 and 2001 (Fig. 5a). In contrast to these findings, Blackburn et al. (1998) examined interspecific relationships among bird species across Britain and reported little variation in the slopes and intercepts among years, with widespread/abundant and restricted distribution/rare species remaining so over their 24-yr data series. This finding did not generate additional tests of this static pattern's generality, even though it was not ascertained whether the stability was the result of true stasis in the positions of species along the interspecific trend, or the narrow variation in abundance and distribution observed within that data series (Gaston et al. 2000).

The current findings demonstrated that if individual species' intraspecific patterns were altered sufficiently, clear changes resulted in the form of the interspecific relationship. As shown in Fig. 6b, a variety of dramatic trajectories were taken by the component species and these changes influenced the interspecific slope. Blackburn et al. (1998) demonstrated that the magnitude of intraspecific changes were not enough relative to interspecific differences to alter the interspecific rank order of birds with respect to the 2 variables through time (see also Newton 1997). However, many of these marine fish species (the majority of which are the target of commercial fishing) displayed wide shifts in both abundance and distribution, resulting in changes in their ranks within the interspecific relationship (Fig. 6b). This history of exploitation is a major distinction between this marine fish assemblage and the assemblage of British birds, and has probably driven the observed changes in the assemblage.

We propose that direct fishery effects and/or second-order trophic effects have influenced the significant changes in the interspecific abundance–distribution slope. Analyses of 60 demersal species revealed significant declines in average body mass between 1970 and 1995 on both the eastern (Divisions 4V and W, 66% de-

cline) and western (Division 4X, 70% decline) Scotian Shelf, which were coincident with increasing fishing effort (Zwanenburg et al. 2002). For individuals in the assemblage, these size decreases would necessitate on average less local resources per individual, leading to the possibility for more individuals to occupy local habitats. If this trend of decreasing body sizes is responsible for the shift in slope, then decreased body size and increased abundance is occurring preferentially for species that have historically been more numerous with larger average distributions. This interpretation is consistent with evaluations of assemblage size-frequency distributions from the Scotian Shelf and other heavily fished areas (Bianchi et al. 2000). Had there been no large-sized removal bias, the effect would have been a positive shift in the average interspecific relationship, rather than the observed increasing slope. Direct fishery effects on species with low abundance and distributions may have also acted on this assemblage if these species were caught incidentally as by-catch. Additionally, species with relatively low abundance and distribution have increasingly been targeted as traditional fisheries have declined (Zwanenburg 2000). This pattern of overfishing abundant, widespread species, followed by targeting lower abundance species with restricted distributions may have contributed to the observed shift in slope at the assemblage level.

Trophic interactions associated with the removal of predators by fisheries may lead to interference by smaller prey species in the recovery rates of large predators (described in the preceding subsection; see Swain & Sinclair 2000, Walters & Kitchell 2001). As well, density compensation, whereby increases in abundance of some species counter the declines of other species (MacArthur 1972), may be operating through increases in prey or competitors of the formerly abundant predator species. Density compensation has been demonstrated in other vertebrate assemblages following exploitation by humans (Peres & Dolman 2000). The relative contributions of increased abundance due to decreased body sizes, the shifting target of commercial fisheries and/or density compensation to the observed change in interspecific relationship, among additional plausible mechanisms, are acknowledged as difficult to quantify using these data, and remain largely speculative. The distinct shift in slopes, however, remains striking. This observed shift in interspecific slope can be tested in other exploited marine and/or terrestrial assemblages and might serve for additional assemblages as an indicator of the recent impact of human or environmental disturbances. The results we report demonstrate that interspecific relationships can be dynamic functions that vary systematically through time, and that these changes are ultimately based on temporal changes in intraspecific trends.

It has been stated that in the study of macroecology there are few ways in which one can experimentally interfere with the functioning of systems at the spatial and temporal scales at which abundance–distribution relationships are documented (Brown 1995, Gaston & Warren 1997). Marine fisheries provide an exception to this general rule. Our results underscore both the large-scale changes that human activity can have on macroecological patterns, and the use of these patterns for the design and evaluation of areas designated for special protection in attempts to re-build depleted stocks.

Acknowledgements. We thank J. A. Hutchings, P. S. Petraitis, N. L. Shackell, D. P. Swain, J. H. M. Willison and the referees for comments on previous versions of the manuscript. Partial support for this research was provided by the Natural Sciences and Engineering Research Council of Canada (K. T. F).

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Editorial responsibility: Howard Browman (Contributing Editor), Storebø, Norway

*Submitted: January 14, 2004; Accepted: June 1, 2004
Proofs received from author(s): September 14, 2004*