

9 Theory and Performance of Ecosystem Models as a Basis for Choosing Metrics of Ecosystem Status and Evaluating Indirect Effects of Fishing

Several modelling approaches were explored, with regard to their ability to provide insight into the ways that fisheries affect ecosystems and their components. First, the various modelling approaches were illustrated in applications prepared by modellers with expertise in the various approaches. These subsections (9.1-9.4) generally present the positive aspects of each approach. A more comparative and critical evaluation of the alternative approaches is presented in Section 9.5, where performance of models are compared to each other, and evaluated against external standards. Limitations as well as potential strengths of model-based approaches to selecting metrics receive more attention in these sections.

9.1 Mass-Balance Models – Theory and Performance

9.1.1 Concepts of aggregate ecosystems models – ECOPATH, ECOSIM, and ECOSPACE

All three of these aggregate ecosystem models were used in the study carried out by Sanchez and Olaso (1999). The use of these models in this study is summarised here by way of an illustration of how they might be applied to examining the indirect effects of fishing on marine ecosystems.

The study used ECOPATH to estimate the following: the trophic level of the fishery, the transfer efficiency between trophic levels, the mixed trophic impact with the fishery as both an impacted and an impacting component, and the historical mean trophic level of the fishery. The input data required were:

- An estimation of biomass (obtained from ICES, ICCAT and survey data in this study; when this value could not be estimated it was back calculated from the model using an alternative value for ecotrophic efficiency (EE) of 0.95);
- An estimation of mortality (obtained from ICES, ICCAT and survey data in this study);
- An estimation of consumption-to-biomass ratios and diet composition of each predator; and
- Landings and discard data from the fishing fleet.

Feeding habits form the links between groups derived from predator-prey relationships determined by stomach content analysis, or from literature values. Discards were considered and 60% were returned to the model (the percent that falls to the seabed), and the 40% taken by seabirds (not included in the model) were accounted for in the category ‘exports’. The model was parameterised as ‘top-down’ such that flow at low trophic levels was set so as to match the food demands of the top levels. Achieving this energy balance assumes a steady-state equilibrium, and is perhaps one of the major drawbacks of the ECOPATH model.

Outputs: Major biomass flow diagram for the studied ecosystem for a given time, showing which groups determine the main flow and which groups form the link between pelagic and demersal groups. The flow of discards can be mapped, and the groups which are most impacted by these discards are identified. This model also provides insight to the direct and indirect trophic interactions within the ecosystem.

ECOSIM is a dynamic extension of ECOPATH (Walters *et al.*, 1997). It includes biomass and size structure dynamics, and uses the same mass balance assumptions as ECOPATH for parameter estimation. The study by Sanchez and Olaso (1999) used ECOSIM to simulate the effect of different fishing regimes on the flow structure of the ecosystem.

Outputs: Data showing the evolution of biomass trends over time for trophic groups as a function of different fishing rates. The relationship between equilibrium biomasses at different fishing levels can thus be graphically displayed. These relationships can be predetermined as being ‘bottom-up’, ‘top-down’ or ‘mixed’ controlled systems. The predictions can also be plotted over time. This representation then shows how different species groups are affected by different levels of trawling and how some populations would decline and others could recover.

ECOSPACE is a mesoscale spatial simulation tool for predicting spatial patterns and runs the ECOPATH model through ECOSIM to model the response of the ecosystem (Walters *et al.*, 1998). Sanchez and Olaso’s (1999) study used ECOSPACE to explore trophic and spatial relationships and to evaluate management options.

The input data required were:

ECOPATH model plus habitat-related parameters, thus replicating ECOSIM dynamics over a spatial grid of 'homogeneous' cells and linking the cells allowing for the dispersal of organisms and changes in fishing effort. ECOSPACE also allows for spatial variation in productivity and can represent habitat 'preferences' according to different criteria (differential dispersal, predation rates, feeding) (Walters *et al.*, 1998).

Outputs: A series of base maps illustrating the evolution of trophic group abundance in different situations. The example of Sanchez and Olaso (1999) illustrates the ecosystem response to a closed area instigated to protect hake recruits.

These three models provided predictions on the functioning of the ecosystem, and can provide predictions about ecosystem effects of each fishery type on different functional groups in the foodweb. This would provide an idea of the importance of each fishery for the trophic dynamics throughout the system.

9.1.2 Case studies using mass-balance models to compare the trophic structure of ecosystems – pelagic upwelling systems

9.1.2.1 Datasets description

A comparison of mass-balance models of trophic flows in the four large marine upwelling areas (Jarre-Teichmann, 1998) was reviewed to illustrate the potential use of this class of models for intersystem comparisons. For this study, the Ecopath II software (Christensen and Pauly, 1992) was used to balance models for different species dominance regimes in the upwelling systems off northern-central Peru (1964–1971 and 1973–1981), California (1965–1972 and 1977–1985), northwest Africa (1972–1979), and Namibia (1971–1977 and 1978–1983). The data for these models had largely been assembled from published literature and/or reports, and the models were built in strictly the same way such as to allow for intersystem comparisons. The study has been expanded since to include the southern Benguela ecosystem as well.

9.1.2.2 Description of the modelling and analysis methodology

9.1.2.2.1 Construction of the models

Assuming mass-balance over an appropriate period of time, the production of each component of an ecosystem (e.g., a sub-population, species or a group of species) is balanced by its predation by other components in the system (predation mortality), its exports from the system (fishing mortality and other exports), and the baseline mortality. Thus,

Production by (i) = All predation on (i) + nonpredatory biomass losses of (i)
+ fishery catches of (i) + other exports of (i)

The terms in this equation may be replaced by

Production by (i) = $B_i * P/B_i$
 Predatory losses of (i) = $\sum_j (B_j * Q/B_j * DC_{j,i})$
 Other losses of (i) = $(1 - EE_i) * B_i * P/B_i$

For any component in the system, this leads to the linear equation

$$B_i * P/B_i * EE_i - \sum_j (B_j * Q/B_j * DC_{j,i}) - Ex_i = 0$$

Where

- i indicates a component (stock, species, species group) of the model,
- j any of the predators of i,
- B_i the biomass of i,
- P/B_i the production i per unit of its biomass (= total mortality under steady-state conditions),
- Q/B_j the consumption of a component per unit of its biomass,
- $DC_{j,i}$ the average fraction of i in the diet of j (in terms of mass),
- EE_i the ecotrophic efficiency of i (the fraction of the total production consumed by predators or exported from the system),

Ex_i the export of *i* from the system (e.g., by emigration, or fishery catch).

The energy balance of each component is given by

$$\text{Consumption} = \text{Production} + \text{Respiration} + \text{Non-assimilated food}$$

wherein consumption is composed of consumption within the system and consumption of imports (i.e., consumption 'outside the system'), and production may be consumed by predators, exported from the system, or be a contribution to detritus.

This structure defines the necessary parameters for the model. For each component, an estimate of its biomass, P/B and Q/B ratios, diet composition, its exports from the system, and its assimilation and ecotrophic efficiencies are required. However, for each component one of the parameters B, P/B, Q/B or ecotrophic efficiency may be unknown, because it is estimated when solving the system of linear equations, along with the respiration of that component. The model is regarded as balanced when realistic estimates of the missing parameters have been achieved for all components of the ecosystem.

Analysis of the models

After a model has been balanced, the various estimates of biomass and turnover rates are checked, and if they are mutually compatible, then the balanced model represents a possible and consistent picture of the energy flows in the system. Only after this process has been completed is it meaningful to perform further analyses of the model, e.g., for interactions between its components and/or the role of the fishery. A rich theoretical framework exists for the analysis of energy flows or cycling in ecosystems, notably building on the theories of Odum (1969) and Ulanowicz (1986). Direct trophic interactions, i.e., predation and fishery, can straightforwardly be assessed by analysing partial mortality coefficients of the prey (or target) groups, and by calculating trophic levels. An additional assessment of indirect trophic interactions, e.g., competition, is possible by mixed trophic impact analysis (Ulanowicz and Puccia, 1990). This approach assesses the relative impact that the change in biomass of a given group would have on the biomass of the other groups in the system. The method is, however, based on the assumption that its trophic structure does not change. Consequently, it is not possible to use it for predictions, but instead as a sensitivity analysis of the cascading effects of changes in an ecosystem's food web.

The partitioning of trophic flows among different consumer groups in an ecosystem can further be illustrative of the role of these consumers in a system, and of their development over time. While fish usually take the largest fraction of fish production (e.g., Bax, 1991; Jarre *et al.*, 1991), the fishery is often the second largest consumer, and often in direct competition with marine mammals.

The fisheries in different ecosystems cannot readily be compared based on their total catch alone, because the species composition of the catch can be rather different. This is in part a result of the specific oceanographic and biological conditions that determine the distribution of a species, but also a result of both fishery management (selection of target species) and fishing practice (selection of fishing gear). Fish are situated at different levels in the food web of an ecosystem, and trophic pathways of different length are therefore required to sustain them. Therefore, the exploitation of fish on lower trophic levels is less expensive in ecological terms than the exploitation of fish on higher trophic levels, and a common currency is needed to compare the ecological cost of fishing among different time periods or systems. Primary production equivalents, as suggested by Pauly and Christensen (1995), are one possibility. Following their approach, a particular end flow in question (e.g., the fishery catch of a species) is traced backwards through the food web, using the ratios of production and consumption of the various components along the path as magnification factors. The sum of the flows leading from the basis of each path (i.e., from the producers' level) to the end flow in question is then the total primary production needed to sustain it.

9.1.2.3 Results

The results of the study indicated that the four upwelling systems ranked rather distinctly after the size parameters primary production, total biomass sustained in the system, fishery catches, and total system throughput (Figure 9.1.3.1). They were set apart in geographical rather than in regime-specific (or temporal) order, although considerable changes in energy flows occurred in some of the systems. Mixed trophic impact analysis showed the importance of primary and secondary production, but also the competition of predatory fish with the fishery, and top-down control aspects like the inhibition of semipelagic fish such as hake through the fishery (Figure 9.1.2.1). The fishery took 20-30% of the production of the five dominant species anchovy, sardine, mackerel, horse mackerel, and hake in all systems except off California where fishing moratoria applied for part of the period under investigation (Figure 9.1.2.2). In this system, a comparatively large fraction of the fish production was consumed by top-predators which are valued more highly by the tourism industry than in the other upwelling areas.

The analysis of primary production required to sustain the fishery (Figure 9.1.2.3) reflected changes in the fishing strategy in systems over time. In the Peruvian system, where the magnitude of the catches was reduced by a factor of more than three between the two periods investigated, the primary production required to sustain the fishery decreased only by 10% as the fishery increasingly targeted hake, a predatory fish, in the later period. The fishery thus remained just as costly in ecologic terms as it had been during the peak period of anchovy exploitation in the 1960s.

9.1.2.4 Discussion

Proponents of these modelling approaches argue that fisheries-oriented construction and analysis of trophic models bear the advantages that:

- (i) they are relatively straightforward to construct,
- (ii) a trophic flow diagram allows to put the commercially exploited species (and the fishery) into the entire ecosystem, giving an immediate visual impact of the trophic flows in the system,
- (iii) a whole toolkit of established methods of network analysis is available to assess, e.g., indirect trophic interactions and top-down control processes,
- (iv) flows can be compared directly between different periods in the same system, or among similarly structured systems.

The comparison of upwelling systems showed, among other results, that the systems are not only driven by food availability as repeatedly suggested, but a number of top-down control mechanisms exists. The position of the small pelagic species in the food web, the low transfer efficiency between trophic levels, and the mixed trophic impact of the lower trophic levels appeared to be rather global properties. By identifying similarities between ecosystems, experiences in their fisheries management could consequently become transferable.

9.1.2.5 References

- Bax, N. 1991. A comparison of the fish biomass flow to fish, fisheries and mammals in six marine ecosystems. *ICES Marine Science Symposia*, 193:217–224.
- Christensen, V., and Pauly, D. 1992. ECOPATH II—a software for balancing steady-state ecosystem models and for calculating network characteristics. *Ecological Modelling*, 61:169–185.
- Jarre-Teichmann, A. 1998. The potential use of mass-balance models for the management of upwelling ecosystems. *Ecological Applications* 8(1), Supplement: 93–103.
- Jarre, A., Muck, P., and Pauly, D. 1991. Two approaches for modelling fish stock interactions in the Peruvian upwelling ecosystem. *ICES Marine Science Symposia*, 193:171–184.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science*, 242:132–1139.
- Pauly, D., and Christensen, V. 1995. Primary production required to sustain global fisheries. *Nature*, 374:255–257.
- Ulanowicz, R.E. 1986. *Growth and development: ecosystem phenomenology*. Springer Verlag, New York. 203 pp.
- Ulanowicz, R.E., and Puccia, C.J. 1990. Mixed trophic impacts in ecosystems. *Coenoses*, 5(1):7–16.

9.1.3 Case studies using mass-balance models to compare the trophic structure of ecosystems – application to the Baltic Sea – 1900 to the present

9.1.3.1 Description of data

The Baltic Sea is a comparatively young, brackish, boreal ecosystem the coasts of which have been inhabited by people for a long time. Primary productivity increased markedly during the past 90 years due to eutrophication. Increased primary production has contributed to approximately a three-fold increase fish biomass from around 1900 to the present (Thurow, 1997). Fishery catches in the Baltic Sea increased about ten-fold in that period. Marine mammals (three species of seals plus harbour porpoise) were abundant at the beginning of this century, but have almost vanished now due to excessive hunting.

As a case study, the seasonal mass-balance models of carbon flows in the central Baltic Sea of Jarre-Teichmann (1995), which were based on Elmgren (1984), Wulff and Ulanowicz (1989), and ICES (1996), were re-arranged to give an annual average of trophic flows at the end of the 1980s, when cod biomass in the Baltic was very low. Food composition of mysids was updated based on Hansson *et al.* (1997). This model of recent trophic flows was compared to a model of carbon flows in the Baltic around 1900, which constructed during the working group based on Elmgren (1989) and Thurow (1997). The ECOPATH software, explained in Section 9.1.2 of this report, was used for balancing and analysing the models. The results of the comparisons are given in Table 9.1.3.1 and in Figure 9.1.3.1.

9.1.3.2 Results and discussion

Odum's (1969) theory divides measures of ecosystem maturity into five groups; community structure and energetics, life history, nutrient recycling, selection pressure, and system homeostasis. Slightly rearranged, measures of (i)

community structure, (ii) structure of the food web, (iii) nutrient cycling, and (iv) system homeostasis were addressed for this case study (Table 9.1.3.1.). A high community production/respiration ratio indicates a rather immature system *sensu* Odum. Production per unit biomass is relatively high although it has decreased during the past 90 years. More biomass is supported per unit energy flow at present, but the fraction is still relatively low. The same holds true for the total biomass in the system. These indicators of community structure point at a rather immature system, as should be expected from the relatively young age in the Baltic.

Connectance index and system omnivory index, both metrics of the diversity of trophic flows in the model, indicate that trophic niches became narrower during the past 90 years, a result well in line with Elmgren's (1989) description of lost food chains due to bottom anoxia in the deeper parts of the Baltic Sea. The loss of the marine mammals as top predators (and their exploitation) resulted in the loss of at least one level in the trophic flow pyramid. However, the average path length in the system remained approximately the same, as cod took over the former role of the mammals. The transfer efficiency of flows between trophic levels increased, which could be an indicator of stress.

Three metrics of food web structure indicate that the food web stayed approximately the same, apart from the loss of some food chains and the mammals as top predators. This is largely due to unchanged flow patterns at the lower trophic levels. It is not clear to what extent this is an artefact of model construction, nor if so, what other implications the artefact would have for model results.

Cycling, nutrient regeneration and the role of detritus in nutrient regeneration all indicate a loss in maturity *sensu* Odum. The loss of maturity could have been caused by both increased primary production (less food limitation) and stress due to pollution. The increasing oxygen depletion in the Baltic in periods of stagnation (no inflow of high saline, oxygen-rich water from the North Sea) has been extensively discussed. However, its effects appear to show in the system summary metrics derived from this relatively simple model.

Summarising, the seemingly contradictory results from the metrics pertaining to community structure and nutrient recycling, respectively, may be explained in the following way. Energy throughput in the Baltic Sea has increased due to eutrophication, making the system 'larger'. With the loss of homeothermic predators, the average organism size has increased along with the increase of fish biomass. However, the additional nutrients appear not to be worked up as well as before, as there is more standing biomass of fish not being consumed by marine mammals. Their mortality leads to a two-fold increase in detritus accumulation and thus, through increased areas suffering from oxygen depletion, to relatively decreased recycling of nutrients.

The metric that within this framework is the closest to being an indicator for system stability, is the system overhead on exports (calculated according to Ulanowicz, 1986). This metric is slightly higher than for large upwelling systems, and lies in the lower range of other shelf ecosystems. The increasing factor of mutual information (Ulanowicz, 1986) points at increasing certainty about the destination of a given unit of flow in the system. This reflects the lower connectance and system omnivory indices, so there are fewer pathways in the system now than earlier. The metrics of system homeostasis thus indicate a shelf-like system, but one which is more vulnerable than typical shelf ecosystems.

The primary production required to sustain the fishery catches increased from 5% at the turn of the century (this already included intense hunting for mammals) to 15% at the end of the 1980s. Although the fishery as a total is probably sustainable in the Baltic, this is only the case because herring and sprat are comparatively lightly fished. Cod, on the other hand, is outside of safe biological limits (ICES, 1997). An assessment of the total ecological cost of the fishery in a system can therefore not replace the assessment of its impact by species, but it can indicate its general compatibility with the flows in the ecosystem.

While mammals consumed about 35% of the total fish production around 1900, their consumption is now lower than 1%. The fishery took slightly less than 11% of the total fish production at the turn of the century, this fraction increased to 36% at the end of the 1980s. Consumption of fish by fish has been relatively constant, approximately 44% of the total fish production. 9% and 19% of fish production were directed to other sinks in the two periods, respectively.

Assuming the same diet composition for mammals as used at the beginning of the century, there would at present be enough food to sustain slightly less than half of their biomass at the turn of the century, i.e., 3 mg C m⁻². The fish production which would be available to mammals appears at present not to be directly consumed in the system, but to enter the detrital food chain. The observation that the seal population in the Baltic is presently increasing at a high rate supports the assumption of available food in the system. However, it is without doubt that the present level of fishing overlaps with the food requirements for mammals at their historic population size. Which of the two forms of consumption in the ecosystem is to be preferred is necessarily a choice of society, balancing, e.g., cultural preferences, economic returns, and a commitment to sustain biodiversity. Whichever the choice, it must be ensured that habitat requirements beyond food supply are also met.

The results of this case study need to be viewed with caution, as the model around 1900 pertains to the entire Baltic Sea, while the model of the late 1980s was constructed for the central Baltic (ICES SDs 25, 26, 28, 29), excluding the western Baltic, Gulf of Riga, the Bothnian Bay, and the Gulf of Finland. However, those conducting the work believe that the trends which emerged here are correct, as it was the more vulnerable areas of the Baltic which were excluded from the more recent model, while the bulk of the fish production has always taken place in the central Baltic Sea. Furthermore, the balancing of the models can only be regarded as preliminary due to time constraints.

The study also showed that the Baltic was far from an unexploited system around 1900, and a considerable further step backwards in time may be required to arrive at a system which was not subject to major anthropogenic influence.

9.1.3.3 Metrics addressing the impact of fishing in this case study

Fishing practices in the Baltic have changed substantially from the beginning of this century. Not only have the catches increased by one order of magnitude, but at the turn of the century a coastal fishery existed which was largely directed towards herring, in combination with seal hunting. At present, the herring fishery continues, but removals of sprat and particularly cod have increased by factors of about 25.

There are three metrics which in the framework of a mass-balance model directly address the impact of a fishery in the ecosystem. The trophic level of the fishery puts the fishery into the ecosystem as a predator, and the models show that the fishery continues to be the top predator in the Baltic Sea. The transfer efficiency between trophic levels, which increased during the past 90 years, reflects the increased productivity (= mortality) of the exploited fish species. The primary production required to sustain the fishery reflects the increased ecological cost of fishing, taking into account the position of the targeted species in the food web (as discussed in connection with comparative modelling of upwelling systems in an earlier section of this report). The increase of the ecological cost of fishing by a factor of three, agrees well with the observed removal of total fish production.

Direct trophic interactions, i.e., predation and fishery, can be assessed directly by analysing partial mortality coefficients of the prey (or target) groups. In addition, mixed trophic impact analysis allows assessment of the indirect trophic interactions, taking into account, e.g., competition of predator groups for prey. The mixed trophic impact of the fishery changed markedly during the past 90 years. Whereas at the turn of the century mammals were strongly impacted by hunting, cod, herring and sprat were only inhibited very lightly. The mixed trophic impact of the fishery on herring increased (in the negative way) by a factor of 5 from the turn of the century to present. A slight inhibition of sprat at the turn of the century turned to a slight favouring (by inhibiting its competitor and predator at present), consistent with observed trends of increasing biomasses in the Baltic. Cod are at present strongly inhibited by the fishery, which shows through an increase of the mixed trophic impact index by an order of magnitude in the negative way.

9.1.3.4 References

- Elmgren, R. 1984. Trophic dynamics in the enclosed, brackish sea. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer*, 193:152–169.
- Elmgren, R. 1989. Man's impact on the ecosystem of the Baltic Sea: Energy flows today and at the turn of the century. *Ambio*, 18(6): 326–332.
- Hansson, S., Hobbie, J.E., Elmgren, R., Larsson, U., Fry, B., and Johansson, S. 1997. The stable nitrogen isotope ratio as a marker of food-web interactions and fish migration. *Ecology*, 78(7):2249–2257.
- ICES. 1996. Report of the Working Group on Multipecies Assessment of Baltic Fish. ICES CM 1996/Assess:2.
- ICES. 1997. Report of the Advisory Committee on Fishery Management, 1997. *ICES Cooperative Research Report No. 223*.
- Jarre-Teichmann, A. 1995. Seasonal mass-balance models of carbon flow in the central Baltic Sea with emphasis on the upper trophic levels. ICES CM 1995/T:6. 26 pp.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science*, 164:262–270.
- Thurow, F. 1997. Estimation of the total fish biomass in the Baltic Sea during the 20th century. *ICES Journal of Marine Science*, 54:444–461.
- Ulanowicz, R.E. 1986. *Growth and development: ecosystem phenomenology*. Springer Verlag, New York. 203 pp.
- Wulff, F., and Ulanowicz, R.E. 1989. A comparative anatomy of the Baltic Sea and Chesapeake Bay ecosystems, pp. 232–256. *In* Network analysis in marine ecosystems. Ed. by F. Wulff, J.G. Field, and K.H. Mann. Springer Verlag, Berlin. 284 pp.

Table 9.1.3.1 Results of the comparison of trophic flows in the Baltic Sea around 1900 and in the late 1980s.

Metric/Period	ca. 1900	ca. 1990
<i>Overview</i>		
Primary production (g cm ⁻² yr ⁻¹)	79	160
Sprat production (g cm ⁻² yr ⁻¹)	0.013	0.258
Herring production (g cm ⁻² yr ⁻¹)	0.112	0.351
Cod production (g cm ⁻² yr ⁻¹)	0.016	0.085
Fishery catches (g cm ⁻² yr ⁻¹)	0.027	0.295
Mammal consumption (g cm ⁻² yr ⁻¹)	0.087	<0.001
Trophic level of the fishery	4.30	4.36
<i>Community structure</i>		
Community P/R (yr ⁻¹)	1.60	1.69
Community P/B (yr ⁻¹)	37.3	16.8
Biomass supported by unit energy flow (g cm ⁻² yr ⁻¹)	0.010	0.017
Net community production (g cm ⁻² yr ⁻¹)	43.5	62.6
Total organic matter sustained (g cm ⁻²)	3.54	9.51
<i>Food web structure</i>		
Connectance index	0.209	0.189
System omnivory index	0.137	0.108
Average path length	3.41	
No. of discrete trophic levels	>8	7
Transfer efficiency between trophic levels	9.3%	12.4%
<i>Nutrient regeneration</i>		
Finn's cycling index (%)	12.6	12.0
Nutrient regeneration (overhead on exports) (%)	4.2	3.6
Role of detritus in nutrient regeneration (%)	59	50
Residence time (B/(R+Ex))		
<i>System homeostasis</i>		
Stability (% system overhead)	71.0	73.0
Information content of flows (bytes per trophic linkage)	1.24	1.89
Primary production required to sustain fishery catches (%)	4.7	14.8
<i>Mixed trophic impact analysis of the fishery</i>		
... impacting sprat	-0.018	0.008
... impacting herring	-0.002	-0.014
... impacting cod	-0.032	-0.275

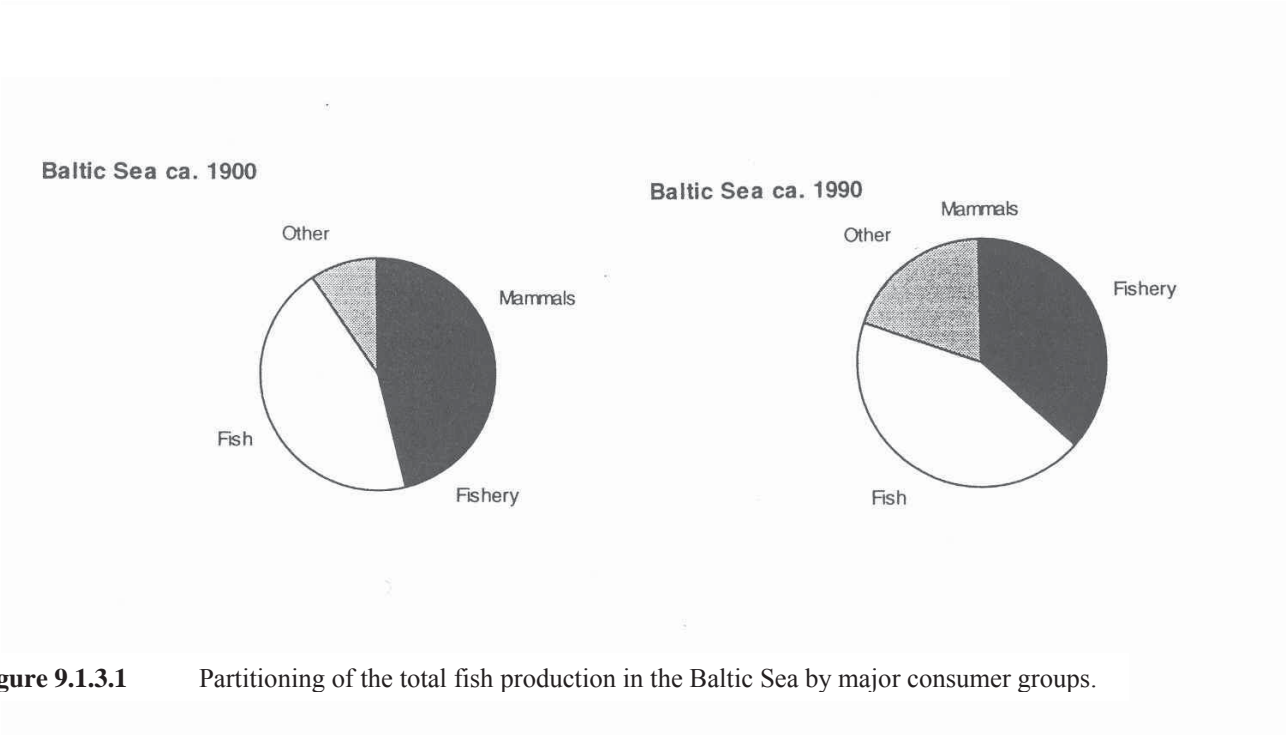


Figure 9.1.3.1 Partitioning of the total fish production in the Baltic Sea by major consumer groups.

9.2 Theory on Size and Diversity Spectra

9.2.1 Size spectra

Studies of the amount of biomass in various size categories has suggested that the logarithm of the biomass in log weight intervals should be approximately constant (Sheldon *et al.*, 1972). Recognizing that the amount of biomass in each size category would depend on the width of the size categories, Platt and Denman (1978) standardized the spectrum by using log biomass divided by the width of the interval on the abscissa and found the standardized spectrum to have a slightly negative slope. Models have been developed which explain the slope and intercepts of the biomass spectrum as a function of the energy-transfer between adjacent trophic levels (e.g., Borgman, 1987; Thiebaut and Dickie, 1993). These models have later been used to predict fish biomass in lakes, but with variable success (Cyr and Peters, 1996).

Fisheries biologists have studied abundance-size rather than biomass-size relations. Pope and Knights (1982) compared the size composition of demersal fish caught by bottom trawl surveys in the North Sea and at the Faroe Islands and found that a straight line fitted log numbers per size class *versus* size in both cases. Subsequent comparisons of size spectra from various parts of the world have confirmed that log numbers per size group often are linearly related to the size of the fish (Pope *et al.*, 1988; Murawski and Idoine, 1992; Gobert, 1994). They have also suggested that the slope of this relationship could be related to fishing intensity. Spectra from areas subjected to different fishing intensities have thus shown that the slope of the size spectra is steeper in heavily fished areas than in less fished areas. The slope is more negative in the heavily fished North Sea than it is in Faroe waters and on the Georges Bank (Pope and Knights, 1982; Murawski and Idoine, 1992). Haedrich and Barnes (1997) linked decreases in biomass and numbers as well as decreases in the mean size of target and non-target species of fish on the northeastern Newfoundland and Labrador shelf to increases in fishing effort. Similar changes in mean size over time was found in analyses of survey data from west Greenland. Analysis of data from two independent bottom trawl surveys in the North Sea revealed an increase in the intercept and a decrease of the slope with time (Section 9.2.3).

In work reviewed at the meeting, for the Bay of Biscay, no significant time trend was found in either slope or intercept of the size spectrum of pelagic and demersal species of fish caught from 1987–1995. When considering only demersal species, a significant increasing trend in the slope and a significant decreasing trend in the intercept was found, but the interpretation was somewhat confounded by significant year/depth strata interactions. Other analyses investigated changes in the species and size composition of the fish catch obtained in five beam trawl surveys in the southern North Sea. The analyses revealed a general increase in the proportion of the smaller size classes of fish in the catch. This increase was tentatively attributed to a decrease in predation leading to an increase in the number of small fish. The findings suggest that the fish assemblage has changed from a top-down regulated assemblage towards a bottom-up regulated assemblage in which increased competition could limit the growth rate of the smaller fish. Although alternative explanations are possible, this interpretation is in accordance with the decrease in weight-at-age of small plaice and the increase in growth of larger plaice (> 35 cm) found by Rijnsdorp and van Leewen (1996).

Section 8.2 of this Chapter provides additional examples of spatial and temporal changes in size spectra within the North Atlantic.

Rice and Gislason (1996) compared the North Sea size spectrum with a size spectrum derived from the numbers at length estimated from the output of MSVPA (Sparre, 1991; ICES, 1997). The changes in the slopes and intercepts of the two spectra were similar. When single and multispecies fish stock assessment models were used to predict changes in the slope and intercept of the size spectrum of the commercially exploited fish in the North Sea in response to fishing it was found that both variables were approximately linear functions of overall fishing effort (ICES, 1996; Gislason and Rice, 1996). The linearity was a consistent feature irrespective of whether a single-species model with constant recruitment was used, a stock recruitment model was added to this model, or a multispecies model (MSFOR) was used to predict the change. In all cases the slope was inversely proportional and the intercept directly proportional to overall fishing mortality. A sensitivity analysis showed that the response of the size spectrum to changes in fishing mortality was virtually unaffected by the level of natural mortality assumed. The response was far more sensitive to changes in growth and stock recruitment dynamics. Changes in growth resulted in major changes in the relationship between fishing mortality and the slope and intercept of the size spectrum. When growth was reduced, the slope and intercept of the size spectrum became much more sensitive to changes in fishing mortality. When growth was increased, sensitivity decreased.

Gislason and Lassen (1997) analysed the mathematical background for the linearity of the change in slope with fishing mortality. Assuming that natural mortality was a function of $1/\text{length}$:

$$M = a + \frac{b_1}{L} + \frac{b_2}{L^2}$$

where:

M: natural mortality
 L: length
 a, b₁, b₂: constants

and that growth could be described by the von Bertalanffy growth equation, and it was shown that the slope of the size distribution for a single-species could be described by:

$$\begin{aligned} slope_{species} &= \frac{\partial \log N(L)}{\partial L} = \\ &= -\frac{b_2}{kL_\infty^2} * \left(\frac{1}{L(t)} + \frac{L_\infty}{L^2(t)} + \frac{1}{L_\infty - L(t)} \right) - \frac{b_1}{kL_\infty} \left(\frac{1}{L(t)} + \frac{1}{L_\infty - L(t)} \right) - \frac{a+f}{k} \left(\frac{1}{L_\infty - L(t)} \right) \end{aligned}$$

where:

N(L): numbers at length
 L_∞, k; von Bertalanffy growth parameters

Differentiating with respect to fishing mortality the rate of change of the slope of the size distribution with fishing mortality could be described by:

$$r_{species} = \frac{\partial^2 \log N(L)}{\partial F \partial L} = -\frac{1}{k} \left(\frac{1}{L_\infty - L(t)} \right)$$

which means that the slope is directly proportional to fishing mortality for a given length. The rate at which the slope will change depends, however, on the growth parameters, but not on natural mortality.

The size distribution of the biomass will respond in a similar way. Assuming standard isometric growth it follows that:

$$\frac{\partial \log B(L)}{\partial L} = \frac{\partial}{\partial L} [\log(q * L^3) + \log N(L)] = \frac{3}{L(t)} + s_{species}$$

The slope of the size distribution of the biomass should therefore respond to changes in fishing mortality in exactly the same way as the size distribution of the numbers.

The size spectrum of the entire fish assemblage is estimated by summing up the abundance at size of the individual species:

$$\log \sum_{species} N_{species}(L)$$

The slope of the assemblage size spectrum is therefore:

$$\bar{s} = \frac{\sum_{species} N(L) \frac{\partial \log N(L)}{\partial L}}{\sum_{species} N(L)} = \frac{\sum_{species} N(L) * s_{species}}{\sum_{species} N(L)}$$

which is equivalent to the weighted (with abundance) mean of the individual slopes. As the individual slopes decrease with increasing fishing mortality the overall slope will also decrease.

For the size spectrum we now have sufficient theoretical and empirical evidence to be confident that changes in fishing mortality should result in a long-term change in the slope of the size spectrum. Provided that the growth and the relative recruitment of the constituent species do not change, the change in the slope should be directly proportional to the change in fishing mortality.

Over shorter time-spans the spectrum will change due to interannual changes in recruitment. Over longer time-spans changes in recruitment levels might also affect the slope. Murawski and Idoine (1992) thus suggested that the size composition was a conservative property of demersal fish assemblages, and that species replacement would counteract the effect of fishing on the size spectrum slope. Similarly it cannot be ruled out that a general environmental change could result in changes in the level of recruitment that were different for large and small species. If the level of recruitment for large species declined relatively to the level of recruitment for small species, the slope of the size spectrum would decrease in a way which might be indiscernible from the influence of an increase in overall fishing mortality. Finally, the response of the spectrum is sensitive to changes in growth, and growth changes might influence the slope of the size spectrum in way similar to fishing. With these possibilities in mind, and interpreted with care, the slope of the size spectrum seems to be a useful indicator of changes in fishing effort.

9.2.2 Diversity spectra

Temporal patterns in species diversity with size have been investigated several times (ICES CM 1994/Assess/Env:1; ICES CM 1996/Assess/Env:1). The rationale behind this work has been that fishing would effect larger slower growing and late maturing species to a larger extent than smaller species with a more rapid turnover. If this is the case, changes in diversity with size are expected with changes in fishing effort. There is now some evidence that this might take place. Analyses have found that the abundance of species with a large size at maturity decreased while those with a small size at maturity increased in beam trawl surveys in the southern North Sea. These results suggest that diversity by size group should change with fishing, but at different rates and possibly even in different directions in different size groups.

Where patterns in diversity by size do show some changes over time, the results are far from easy to interpret and difficult to link theoretically to fishing effort. Indeed, the modelling study of Gislason and Rice (1996) suggests that the diversity spectrum would be among the less useful measures of changes in fishing effort. The way in which the slope and intercept of the diversity spectrum changed with fishing effort differed between single-species models with and without stock/recruitment relationships and multispecies (MSFOR) models. Furthermore, none of the models predicted the higher evenness at low levels of fishing mortality suggested by the analyses of survey data from the North Sea from 1906–1909 and 1990–1995 made by Rijnsdorp *et al.* (1996).

Furthermore, species diversity is assessed with a multitude of diversity indices. Each of these indices combines information on species richness and evenness into a single number. High evenness occurs when species are equal or approximately equal in abundance, low evenness when the species composition is dominated by a few abundant species. Due to the relative importance each index gives to evenness and richness, it is difficult to compare the indices. A Working Paper by Rogers *et al.* (in press) compared diversity of coastal demersal fish faunas in the northeast Atlantic by diversity profiles calculated from:

$$H_{\alpha} = (\log \sum_i p_i^{\alpha}) / (1 - \alpha)$$

Substituting 0.1 and 2 for the scale parameter α , H_{α} , will be directly related to species richness, Shannon's entropy and Simpsons dominance index, respectively. Thus for α near zero, the index will be dominated by richness, while for larger values of α , species evenness will have progressively more effect.

Without a theory to provide a causal link between fishing intensity and diversity, it will be difficult to know whether diversity is a useful measure of fishing impact. Recent work by Hall and Greenstreet (2000) suggests, however, that there are patterns in relationships between species richness, individual abundance, and size which might be linked to fisheries effects at the community level.

Hall and Greenstreet described the relationships between species diversity, the abundance of individuals, and body size in a demersal fish community. They investigated patterns in different geographic regions in the northwestern North Sea and over a 60-year period. A striking similarity with previously reported data for insect communities was observed. A dome-shaped relationship between both species richness (S) and individual abundance (I) with body size was found when data were categorised in logarithmic (to base 2) weight classes. The same power law relationship between S and I, of the form $S = aI^b$, existed for both types of fauna. The coefficient b of this relationship did not differ between regions or over time, whereas the intercept a declined over time. This decline could not be accounted for by sampling artefacts and Hall and Greenstreet suggest that it may provide an informative measure of the effect of fisheries exploitation on the community. They also demonstrated that rank abundance relationships within body size classes exhibited a similar pattern to that found in insects, of the form $A = r - m$ (where A = abundance and r = species rank). These similarities with insects and the robustness of the patterns for fish when compared over large spatial (100 km) and temporal (decadal) scales, suggest that common explanations may underlie the organisation of these communities. With respect to fisheries effects, it would appear from these data that the coefficient a of the power law relationship $S = I^b$, when data are categorised into weight classes, might be a valuable measure of the effect on fish species assemblages of fishing disturbance.

The empirical studies of changes in species diversity have been inconsistent and the theoretical understanding has not advanced to a state where the underlying process can be modelled. More work is therefore needed before predictions can be made about how fishing would affect the diversity spectrum.

9.2.3 Diversity profiles

Improvements in the measurement and interpretation of diversity have recently been made using methods of diversity ordering (Tothmeresz, 1995), where a range of diversity indices within a family show varying sensitivities to rare and abundant species. These profiles display graphically a family of diversity indices obtained by changing the scale parameter a . There are several available, but one that is recommended for large datasets is Renyi's diversity index family.

$$H_a = (\log \sum p_i^a) / (1 - a)$$

When substituting 0, 1, and 2 for the scale parameter a , H_a will be directly related to the species richness (i.e., is the log. of the species number), Shannon's entropy and Simpsons dominance index, respectively (Hill, 1973). Thus for a near zero, richness will have more effect on H_a , but for larger values of the scale parameter, species evenness has more effect. For scale parameters which increase from 1 to 4 the influence of rare species will be gradually replaced by the influence of dominant species. One community is more diverse than another if its' diversity profile is equal to or above that of another, over the whole range of the scale parameter. If the two profiles intersect at any point then they can be considered non-comparable (i.e., different diversity indices would rank the communities differently).

Diversity profiles were calculated for the demersal fish catches (number/8m beam trawl/hour) from the coastal waters of the northeast Atlantic (Rogers *et al.*, in press). Results suggest that this is a robust technique for identifying differences in diversity between assemblages, which takes account of all combinations of species richness and evenness.

9.3 Community metrics models

These models begin with basic concepts from community ecology, developed primarily in terrestrial ecosystems, and attempt to represent marine ecosystem dynamics that would follow from the community processes.

9.3.1 Huston's Dynamic Equilibrium Model

Initial theoretical community ecology models presupposed that the species diversity of communities was underpinned by competitive exclusion until ultimately competitive equilibrium was achieved (MacArthur, 1970; MacArthur and Levins, 1967). Many early studies supported these ideas (e.g., Park, 1948, 1954; Pianka, 1973, 1975, 1983; Fenchel, 1975; Davidson, 1977), but not all. Communities were identified which, while apparently stable, were clearly not at competitive equilibrium (e.g., Paine, 1966; Patrick, 1975). These suggested that predation was the dominant process governing the structure of communities. In its absence communities progressed to competitive equilibrium, in its presence an alternative stable, or even unstable, state existed (e.g., Connell, 1975). The apparently opposing effects of competition and predation led Huston (1979) to propose the 'dynamic equilibria model' of species diversity, the fundamental predictions of which are encompassed in Figure 9.3.1.1. Huston considered predation to be simply one source of 'disturbance', i.e., a factor that caused mortality and limited the scope for population growth. In the application of this model, fishing can be considered as a disturbance resulting in mortality, causing at worst, reductions in population size, or at best, limiting the extent of population increase. Variation in productivity puts limits on the amount of food resources available to competing predators.

The theory assumes a unimodal response of species diversity to both disturbance and productivity. Thus for example, nutrient enrichment events have been shown to result in both increases and decreases in species diversity (e.g., Mirza and Gray, 1981; Russo, 1982), i.e., both limbs of the unimodal relationship. At low disturbance frequency, diversity is highest at the intermediate to low end of the productivity spectrum. At the lowest productivity, population growth is so slow that extinction is a distinct possibility. At higher productivity, the scope for growth is sufficiently high that the populations of the dominant competitors will be able grow fast enough, so as to be able to capture an increasingly unequal share of the resources. Growth of the subordinate competitors will be impeded and they will be excluded before the next disturbance occurs. At higher disturbance frequencies, diversity will be lower at low productivity levels; some populations will be unable to grow fast enough to recover sufficiently between disturbance events and they will be driven to extinction. At intermediate productivity levels, populations will be able to grow fast enough to avoid extinction, but the growth of the dominant competitors will be checked, so preventing competitive exclusion. Species diversity in areas of high disturbance frequency and high productivity will be lower than in areas of intermediate levels of both because the high frequency of disturbance is likely to eliminate k -selected species and so reduce the total species pool available. Huston (1994) examined a large number and variety of species assemblage data sets and generally found that variation in species diversity could be explained in terms of the dynamic equilibria model.

What insight can this model provide regarding the impact of fishing disturbance on North Sea groundfish species assemblages? Figure 9.3.1.2 shows that the relationship between diversity and disturbance is strongly influenced by environmental productivity. Consider an increase in disturbance over the range of 20 to 80 units at the three levels of productivity marked on Figure 9.3.1.1. In productive environments increasing disturbance results in increased species diversity, while in unproductive environments the opposite trend is observed. In moderately productive environments diversity increases as disturbance rate increases to intermediate levels, thereafter diversity decreases. Secondly, the model suggests that without accounting for variation in productivity in some sort of multivariate analysis, it could prove difficult to determine any relationship at all. Figure 9.3.1.3 looks at the mean (and standard deviation) species diversity predicted by the dynamic equilibrium model at various disturbance levels over the whole productivity range. The three levels of fishing disturbance shown on Figure 9.3.1.1 are indicated. This graph suggests that we would be very unlikely to detect any significant variation in species diversity among the three fishing disturbance regimes from sets of random samples taken across the full productivity range. Finally, Figure 9.3.1.4 examines the response of species diversity to variation in productivity at the three levels of fishing disturbance indicated on Figure 9.3.1.1. In low productivity environments, species diversity is highest at low disturbance and least at high disturbance, a ranking which intuition suggests might be expected. However, at intermediate productivity the ranking starts to alter, so that where productivity is high the order is completely reversed; diversity is greatest where disturbance is most prevalent and *vice versa*.

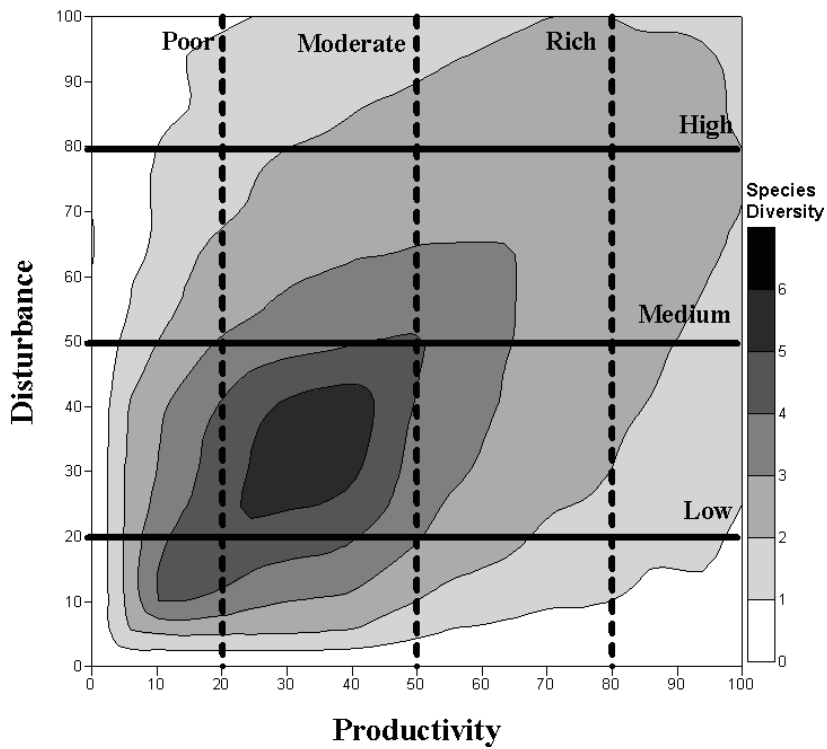


Figure 9.3.1.1 Huston's (1979) 'dynamic equilibria model' of species diversity.

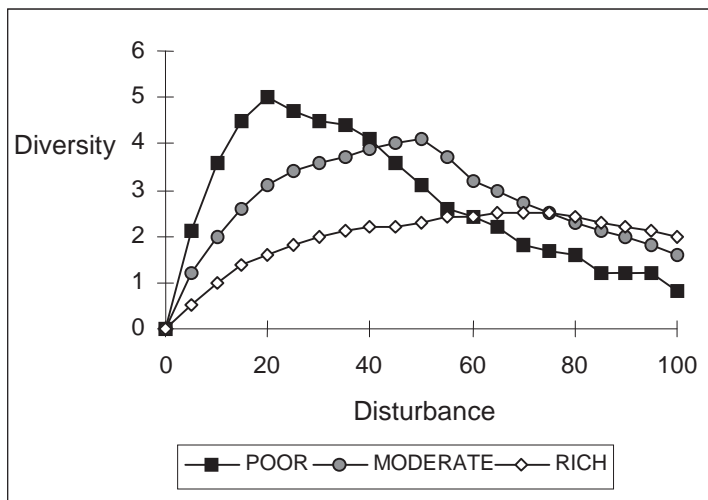


Figure 9.3.1.2 Relationship between species diversity and fish disturbance intensity at three levels of environmental productivity.

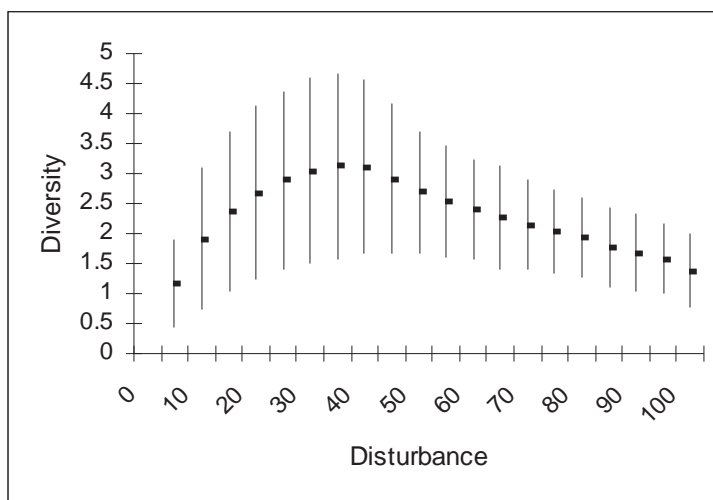


Figure 9.3.1.3 Effect of disturbance on the mean diversity and standard deviation estimated over the full productivity range. Low, medium, and high disturbance ranges shown on Figures 9.3.1.2 and 9.3.1.4 correspond to regions labelled low, medium, and high in Figure 9.3.1.1.

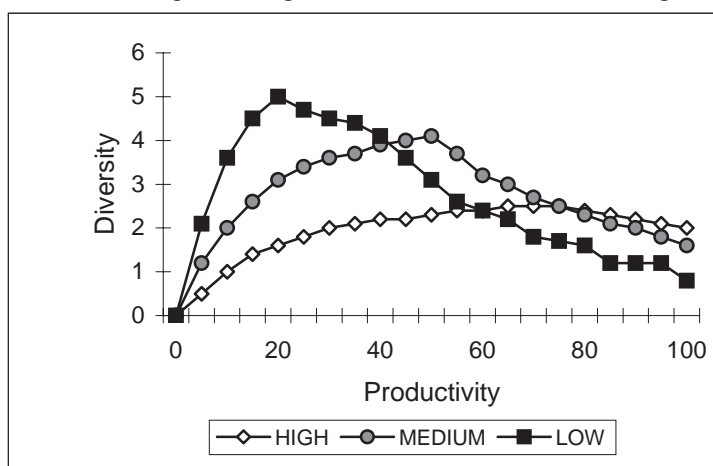


Figure 9.3.1.4 Relationship between species diversity and productivity at three fishing disturbance intensities.

The effects of disturbance on community species diversity are thus far from clear-cut (e.g., Death and Winterbourn, 1995). They may be particularly complex in marine ecosystems (Russo, 1982; Menge and Sutherland, 1987), underlining the necessity for the provision and validation of underlying theory. One of the difficulties in applying such models, however, is the frequent absence of the necessary data to fully parameterize it, in this case a direct measure of system productivity. One approach would be to find suitable correlates, such as water depth in marine systems (Rosenzweig and Abramsky, 1993). However, the use of such substitutes requires caution (Rosenzweig, 1995). A second approach may be to use empirical relationships (e.g., Brey, 1990; Duineveld *et al.*, 1991; also see Bryant *et al.*, 1995) to estimate benthic production from benthic standing crop biomass data. Such data may be available for the North Sea, at least in basic form, collected during the ICES North Sea Benthos Survey (Heip *et al.*, 1992; Basford *et al.*, 1993), and additional data continue to be collected. This raises the possibility of examining the relationships in spatial variation in fishing disturbance, benthic production and demersal fish species diversity to explore the value of Huston's model as a tool to enable us to predict the consequences of changes in fishing practice on groundfish species diversity.

9.3.2 An age/size-structured ecosystem model—European Regional Seas Ecosystem Model (ERSEM)

Most of the early models used to describe energy/carbon/nitrogen flow through marine food webs essentially assumed a steady-state dynamic equilibrium situation; they were 'static' models (e.g., Steele, 1974; Billen, 1978; Jones, 1982, 1984; Cohen *et al.*, 1982; Mommaerts *et al.*, 1984). The alternative view is that the food web is not at equilibrium and is instead constantly responding to environmental and/or anthropogenic forcing. Describing such situations required the application of 'dynamic' time-evolving models (Fransz and Verhagen, 1985; Billen and Lancelot, 1988). Both of these approaches require simplified representation of the ecosystem by the aggregation of species into functional groups. The degree of species aggregation varies considerably between models. An overview of many of these earlier models is provided by Fransz *et al.* (1991).

More recently many research institutes around the North Sea were involved in a project to develop a spatially explicit model of carbon pathways through the North Sea ecosystem (Baretta *et al.*, 1995). The model used the ten ICES areas to achieve a relatively coarse spatial resolution. The five offshore boxes were split into two by depth to model the effect of the thermocline. Primary production occurred in the upper box, whilst the lower box included the links to the benthos. A general circulation model was used to generate daily horizontal exchange rates of dissolved and suspended constituents between the ten surface boxes. Vertical transport between the five upper and lower boxes was based on determined sinking rates for the sedimentation of particulates and turbulent diffusion for the dissolved constituents.

The physical model contained information specific to the area to be modelled, whereas the biological/chemical sub-models were constructed to be non-site-specific. The biological variables were represented as functional groups expressed as units of organic carbon and the chemical variables as internal pools in the biological variables and as dissolved inorganic pools in the water and the sediment, expressed in units of N, P, and Si.

The model is modular in its construction, with each module dealing with a related collection of functional groups, thus the Zoobenthos model included the functional groups: Benthic Carnivores; Suspension Feeders; Deposit Feeders; and Meiobenthos. The modules were set up to run within the ten ICES boxes and the five lower layer boxes using the Software Environment for Simulation and Analysis of Marine Ecosystems (SESAME) (Ruudij *et al.*, 1995). The modules were linked to allow the exchange of carbon and nutrients between the modules. These were then routed through the functional groups comprising each module. Size and age structure was explicitly represented in the fish groups, but the remaining biological components were modelled as unstructured populations. This was deemed appropriate for taxa having short generation times relative to the annual cycle, and for taxa which did not cross more than one trophic level in their lifetime.

This model has not been used to examine the indirect effects of fishing on the emergent properties of the ecosystem. However, it would be a relatively easy step to introduce some rate of fishing mortality to the age-structured fish module. Such mortality could even be applied to take into account spatial and seasonal variation in the behaviour of different fisheries. The consequent changes arising from alteration to the carbon flow through the various modules could then be tracked over any given time period (1 to 10 years, or longer if appropriate). Examples of the sort of ecosystem food web alterations for which predictions could be obtained are: the consequences of sandeel fisheries operating in specific locations to top predators in the area, and to the zooplankton populations on which the sandeels prey. Furthermore, predictions could also be obtained regarding the effects of all these higher trophic level changes on the benthos-pelagic coupling in the system.

9.4 Evaluating Ecosystem Effects of Fishing: Predictions from Ecosystem Dynamics Models

Building on the illustrations of the major modelling approaches, WGECO next used the principal models of ecosystem dynamics to develop specific predictions regarding the ecosystem effects of fishing;

9.4.1 Inventory of models of ecosystem dynamics

There has been a multitude of models constructed, each of which purports to illustrate the dynamics of ecosystems. A useful classification of these models was provided by a flowchart in Hollowed *et al.* (2000) (Figure 9.4.1). This flow chart provides a useful guide to grouping together models based on similar constructs, requiring similar input variable data and producing similar output predictions. We have used this flow chart to produce the key to ecosystem models presented in Sections 9.3.1-9.3.3, and other models from the literature. We have used the key to assign models gleaned from the theoretical ecology and fisheries science literature to various categories or 'families' of models. Models within a family will provide essentially the same sort of insight into how fishing may affect the ecosystem. It may be that each model may require slightly different input data, thus some models within a family may be more or less appropriate, or practical, when attempting to address a particular issue. Different families of models will essentially address different issues, or provide different insights into ecosystem operation. Chapter 1 concluded that there is no evidence that we will fail to safeguard the marine ecosystems as long as single-species issues are addressed adequately, such that no one component or species within the ecosystem is subject to unsustainable mortality, and habitats are protected. This message is confirmed in our current deliberations. Only a few of the models mentioned below consider single-species in a way that can be directly compared with current assessment models, dealing as they do in the most part with multispecies interactions. Multispecies models therefore provide a means of examining how fishing disturbance might affect the emergent properties of ecosystems, in particular food-web dynamics and change in species diversity. This, in turn, might provide the definitive answer to questions about the risk posed to emergent ecosystem properties in systems where individual species are not at risk. In Section 9.4 we briefly describe some of the models in each of the model families defined by the key. We indicate what they do, some of the key assumptions, and the type of output they provide.

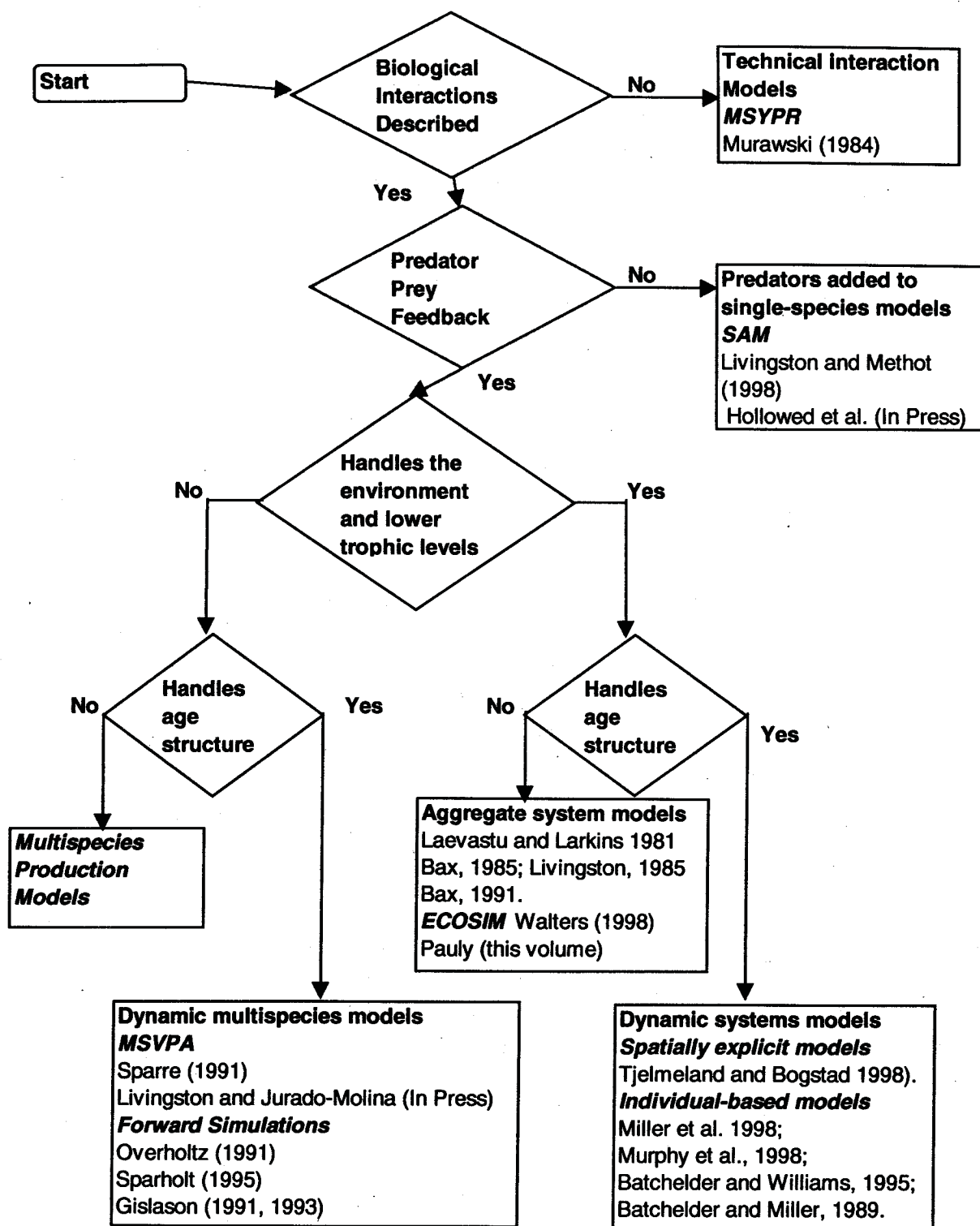


Figure 9.4.1 Flow chart summarizing classification of multispecies models. **Bold** letters indicate model classification, *italicized* letters indicate sub-categories of models. References for classes and sub-categories of models are provided in the text of the paper by Hollowed *et al.* (2000).

9.4.2 Model type key

- 1) Is habitat suitability explicitly included?
 - No go to 2
 - Yes Basin model (MacCall, 1990)
- 2) Is model based on community metrics?

- No go to 3
 Yes Dynamic equilibrium model (Huston, 1979, 1994)
 Size-spectrum model (Pope *et al.*, 1988)
- 3) Predator-prey-feedback included?
 No Prey added to single-species models (Furness, 1978)
 Predators added to single-species models (Livingston and Methot, 1998)
 Yes go to 4
- 4) Are the environment and lower trophic levels included?
 No go to 5
 Yes go to 7
- 5) Age structure?
 No Multispecies production models
 a. Multispecies Lotka-Volterra models (May *et al.*, 1979)
 b. Predator-prey models with non-linear interactions (Collie and Spencer, 1994; Spencer and Collie, 1996; Basson and Fogarty, 1997)
 c. Spatially-explicit predator-prey models (Pascual and Levin, 1999)
 Yes go to 6
- 6) Dynamic multispecies models with age-structure [a], variable growth [g], multiple fleets [f], spatial structure [s]
 a. MSVPA (Sparre, 1991) [a, f]
 b. MSGVPA (Gislason, 1999) [a, g, f]
 c. Length-based MSVPA (Dobby *et al.*, 1999) [g, f]
 d. MULTSPEC (Tjelmeland and Bogstad, 1998) [a, f, g, s]
 e. Bormicon (Stefánsson and Pálsson, 1997) [a, f, g, s]
 f. 4M (Vinter and Thomsen, 1998) [a, f, g, s]
- 7) Age-structured?
 No go to 8
 Yes go to 9
- 8) Aggregate system models with time dynamics [t], spatial dynamics [s]
 a. N→P→Z models
 b. ECOPATH (Polovina, 1984)
 c. ECOSIM (Walters *et al.*, 1997) [t]
 d. ECOSPACE (Walters *et al.*, 1998) [t,s]
- 9) Age/size structured ecosystem models
 a. Andersen and Ursin (1977) North Sea model [t]*
 b. ERSEM (Baretta *et al.*, 1995) [t, s]
 c. Individual based models (Murphy *et al.*, 1998; Batchelder and Williams, 1995)
 d. OSMOSE (Shin and Cury, 1999) [a, t, s]

9.4.3 Description of models and predictions for the ecosystem effects of fishing

The classes of models correspond to the key above. We list the principal properties of each class of model without reviewing their validity or usefulness. Generic predictions are made about the ecosystem effects of fishing if each of the models were a correct description of the ecosystem. Several of the models have been described more fully in Section 9.2. A more thorough review will require a more complete description of each model's properties, consideration of the underlying assumptions or theory, and empirical evidence for the model. For those models that have been implemented and parameterised, estimates of the ecosystem effects of fishing can be made.

Habitat-based models

Properties

The population growth rate depends on habitat suitability. Realised suitability is a function of local population density. Individuals distribute themselves with an ideal-free distribution such that realised suitability is equal over the entire range of habitats (see MacCall, 1990).

*This model is no longer in use.

Predictions

As fishing reduces the total population size, the population range will contract to the most suitable habitats. Catchability will remain constant in the core habitat as total population size declines because local population density is highest in the most suitable habitats.

Models based on community metrics

Properties

These models are generally applied at the community level and do not describe the abundance of individual species from one generation to the next. According to the dynamic-equilibrium model, species diversity is a function of ecosystem productivity and natural disturbance levels (see more detailed description of this model in Section 9.3.1). The size-spectrum model describes the decrease in number of individuals with increasing length classes.

Predictions

The dynamic equilibrium model predicts that species diversity will change in response to fishing disturbance. The direction and magnitude of the change depends on levels of production and natural disturbance in the unimpacted ecosystem. The slope of the size spectrum is expected to become steeper when the community is exploited. The relationship between the slope of the size spectrum and fishing mortality has been investigated by simulation (Gislason and Lassen, 1997) and by comparing the size spectra from fish communities around the world (Bianchi *et al.*, in press).

Single-species models with variable prey or predators

Properties

These are dynamic single-species models with either variable prey abundance (e.g., fish abundance for seabirds) or variable predator abundance (e.g., predators on fish populations). Trophic feedback is in one direction only.

Predictions

In the case of variable prey, harvesting the prey species (forage fish) will reduce the reproductive rate or growth rate of the predators (seabirds). In the case of variable predation, harvesting the predator will reduce the natural mortality of the prey species and may lead to higher prey recruitment (Walters *et al.*, 1986). Harvesting the prey would not affect the predators because of the lack of prey-predator feedback. These models could perhaps be used to examine some of the immediate effects of alteration in the abundance of particular single-species, i.e., the type of change which has commanded most attention throughout the remainder of the report.

Multispecies production models

Properties

The simplest examples derive from the Lotka-Volterra model and have first-order linear interaction terms. Density-dependent regulation of the prey is necessary for system stability.

Predictions

Harvesting the predator increases prey abundance and hence the potential prey yield (May *et al.*, 1979). Harvesting the prey reduces predator abundance and the potential predator yield.

Predator-prey models with non-linear interactions

Properties

Non-linear functional responses and time delays in the effects of predation can give rise to multiple equilibrium levels of predators and prey populations. With a type-two predator functional response, there may be two equilibria: a stable upper equilibrium and a lower unstable equilibrium. With a type-three predator functional response, there may be two stable equilibria separated by an unstable equilibrium (Steele and Henderson, 1981). Habitat suitability can be linked to species carrying capacity (Sainsbury, 1991).

Predictions

The effects of fishing are generally the same as for other multispecies production models (see above). In addition, incremental changes in either the predator or prey exploitation rates can cause the system to flip rapidly from one equilibrium level to the other (Collie and Spencer, 1994; Spencer and Collie, 1996). Prey populations can get trapped in 'predator pits' such that recovery may be delayed and require substantial reductions in fishing mortality. Fishing can reduce habitat suitability and selectively reduce the abundance of species which depend on that feature of the habitat (Sainsbury, 1991).

Dynamic spatially structured multispecies models

Properties

Predator-prey dynamics are simulated at small spatial scales. The spatial structure may include prey refugia. The dynamics of the populations can be examined by aggregating the spatial grid into larger 'windows.' Such models can exhibit oscillatory behaviour and multiple equilibria when examined on intermediate spatial scales.

Predictions

Spatial models of this type generally have not explicitly included fishing, but fishing mortality could be added.

Dynamic age/size-structured multispecies models

Properties

These models track the fates of cohorts backward in time (MSVPA, MSGVPA, 4M) or forward from recruitment (Multspec, Bormicon). Natural mortality is a dynamic function of predator abundance and prey availability. Length-based MSVPA removes the dependence on age-length keys by incorporating growth models. In the models with variable growth rates, size at age is a function of food availability, as observed in boreal ecosystems. Models with spatial structure explicitly consider the seasonal overlap between predators and their prey.

Predictions

Harvesting the predators reduces natural mortality of the prey species, resulting in increased prey abundance and increased potential prey yields. In models with variable growth, harvesting the prey will reduce predator growth rates, resulting in reduced predator biomass and potential predator yields. The indirect effects of harvesting one species on other species in the community may be positive or negative depending on the food web structure. Spatially explicit models allow for local depletion of prey abundance ('understocking') even when total prey abundance remains undepleted.

Aggregate ecosystem models

Properties

These models derive from food webs and energy budgets; the units may be energy, carbon or biomass. Species are aggregated into functional groups, especially at the lower trophic levels. The trophic interactions are generally first-order linear. Static mass-balance models (e.g., ECOPATH) assume that the production of each ecosystem component is balanced by losses due to predation, non-predation mortality and export. Dynamic ecosystem models require some form of density dependence to prevent species extinctions. In ECOSIM, this stabilisation is provided by partitioning the functional groups into available and unavailable pools (Walters *et al.*, 1997). Spatially explicit ecosystem models (e.g., ECOSPACE) can model prey availability explicitly and can also define habitat suitability.

Predictions

In static ecosystem models, fishing mortality must be balanced by increased production or reduced predation on that functional group. Dynamic ecosystem models can describe the time dynamics of these changes to a new steady state. In general, harvesting a functional group will reduce its own biomass and the biomass of those groups that feed on it, while increasing the biomass of those groups which are preyed on. These changes can propagate along the food chain, resulting in a trophic cascade (Carpenter *et al.*, 1985).

Age/size-structured ecosystem models

Properties

This class of models is distinguished from the aggregate ecosystem models in that the individual functional groups are generally less aggregated and their dynamics are described with greater temporal resolution. Given the high level of detail, these models are often constructed as simulations and individual based models (e.g., Shin and Cury, 1999) as opposed to statistical models fit to data. Coupled biophysical models that incorporate flow fields concentrate on the lower trophic levels and planktonic life stages.

Predictions

Many of the existing models of this type do not include the upper trophic levels (i.e., fish) and therefore cannot be used to predict the effects of fishing in their present form.

9.5 References

- Andersen, K.P., and Ursin, E. 1977. A multi-species extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Meddelelser fra Danmarks Fiskeri- og Havundersøgelser*. N.S., 7: 319–435.
- Baretta, J.W., Ebenhoh, W., and Ruardij, P. 1995. The European regional seas ecosystem model, a complex marine ecosystem model. *Netherlands Journal of Sea Research*, 33: 233–246.
- Basford, D.J., Eleftheriou, A., Davies, I.M., Irion, G., and Soltwedel, T. 1993. The ICES North Sea benthos survey: the sedimentary environment. *ICES Journal of Marine Science*, 50: 71–80.
- Basson, M., and Fogarty, M.J. 1997. Harvesting in discrete-time predator-prey systems. *Mathematical Biosciences*, 141 (1): 41–74.
- Batchelder, H.P., and Williams, R. 1995. Individual-based modelling of the population dynamics of *Mertridia lucens* in the North Atlantic. *ICES Journal of Marine Science*, 52: 469–482.
- Bianchi, G., Gislason, H., Graham, K., Hill, L., Koranteng, K., Manickchand-Heileman, S., Paya, I., Sainsbury, K., Sanchez, F., Jin, X., and Zwanenburg, K. In press. Impact of fishing on demersal fish assemblages. *ICES Journal of Marine Science*.
- Billen, G. 1978. A budget of nitrogen cycling in North Sea sediments off the Belgian coast. *Estuarine and Coastal Marine Science*, 7: 127–146.
- Billen, G., and Lancelot, C. 1988. Modelling benthic nitrogen cycling in temperate coastal ecosystems. *In Nitrogen Cycling in Coastal Marine Environments*, pp. 343–378. Ed. by T.H. Blackburn and J. Sorensen. Wiley and Sons Ltd., London.
- Borgman, U. 1987. Models on the slope of, and biomass flow up, the Biomass Size Spectrum. *Can. J. Fish. Aquat. Sci.*, 44(Suppl.2): 136–140.
- Brey, T. 1990. Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. *Meeresforschungen*, 32: 329–343.
- Bryant, A.D., Heath, M.R., Broekhuizen, N., Ollason, J.G., Gurney, W.S.G., and Greenstreet, S.P.R. 1995. Modelling the predation, growth and population dynamics of fish within a spatially-resolved shelf sea ecosystem model. *Netherlands Journal of Sea Research*, 33: 407–421.
- Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. *BioScience*, 35: 634–639.
- Cohen, E.B., Grosslein, M.D., Sissenwine, M.P., Steimle, F., and Wright, W.R. 1982. Energy budget of Georges Bank. *In Multispecies Approaches to Fisheries Management Advice*, pp. 95–107. Ed. by M.C. Mercer. Canadian Special Publication in Fisheries and Aquatic Science, 59.
- Collie, J.S., and Spencer, P.D. 1994. Modeling predator-prey dynamics in a fluctuating environment. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 2665–2672.
- Connell, J.H. 1975. Some mechanisms producing structure in natural communities. *In Ecology and Evolution of Communities*, pp. 460–490. Ed. by M.L. Cody and J.M. Diamond. Belknap Harvard University Press, Cambridge, Massachusetts.
- Cyr, H., and Peters, R.H. 1996. Biomass-size spectra and the prediction of fish biomass in lakes. *Can. J. Fish. Aquat. Sci.*, 53: 994–1006.
- Davidson, D.W. 1977. Species diversity and community organization in desert seed-eating ants. *Ecology*, 58: 711–724.
- Death, R.G., and Winterbourn, M.J. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology*, 76: 1446–1460.
- Dobby, H., Veitch, A.R., Banks, D., and Gurney, W.S.C. 1999. Incorporating length-based predation into multispecies fisheries modelling. Submitted for publication.
- Duineveld, G.C.A., Kunitzer, A., Niermann, U., de Wilde, P.A.W.J., and Gray, J.S. 1991. The macrobenthos of the North Sea. *Netherlands Journal of Sea Research*, 28: 53–65.
- Fenchel, T. 1975. Character displacement and coexistence in mud snails (Hydrobiidae). *Oecologia*, 20: 19–32.
- Fransz, H.G., Mommaerts, J.P., and Radach, G. 1991. Ecological modelling of the North Sea. *Netherlands Journal of Sea Research*, 28: 67–140.
- Fransz, H.G., and Verhagen, J.H.G. 1985. Modelling research on the production cycle of phytoplankton in the Southern Bight of the North Sea in relation to river-borne nutrient loads. *Netherlands Journal of Sea Research*, 19: 241–250.
- Furness, R.W. 1978. Energy requirements of seabird communities: a bioenergetics model. *Journal of Animal Ecology*, 47(1): 39–53.
- Gislason, H. 1999. Biological reference limits for interacting species in the Baltic. *ICES Journal of Marine Science*, 56: 571–583.
- Gislason, H., and Rice, J. 1996. Modelling the effect of changes in fishing effort on the size and diversity spectra of exploited fish assemblages. *ICES CM 1996/Mini:15*.
- Gislason, H., and Lassen, H. 1997. On the linear relationship between fishing effort and the slope of the size spectrum. *ICES CM 1997/DD:05*.
- Gobert, B. 1994. Size structures of demersal catches in a multispecies multigear tropical fishery. *Fisheries Research*, 19: 87–104.

- Haedrich, R.L., and Barnes, S.M. 1997. Changes over time of the size structure in an exploited shelf fish community. *Fisheries Research*, 31: 229–239.
- Hall, S.J., and Greenstreet, S.P.R. 2000. Submitted. Diversity, abundance and body size in fish: how robust are the patterns and what do they tell us? *American Naturalist*.
- Heip, C., Basford, D., Craeymeersch, J.A., Dewarumez, J.-M., de Wilde, P., Dorjes, J., Duineveld, G., Eleftheriou, A., Herman, P.M.J., Niermann, U., Kingston, P., Künitzer, A., Rachor, E., Rumohr, H., Soetaert, K., and Soltwedel, T. 1992. Trends in biomass, density and diversity of North Sea macrofauna. *ICES Journal of Marine Science*, 49: 13–22.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54: 427–432.
- Hollowed, A.B., Bax, N., Beamish, R., Collie, J.S., Fogarty, M., Livingston, P., Pope, J., and Rice, J. 2000 In press. Are multispecies models an improvement on single-species models for measuring impacts on marine ecosystems? *ICES Journal of Marine Science*.
- Huston, A.H. 1979. A general hypothesis of species diversity. *American Naturalist*, 113: 81–101.
- Huston, A.H. 1994. *Biological diversity: The coexistence of species on changing landscapes*. Cambridge University Press. 681 pp.
- ICES. 1996. Report of the Working Group on Ecosystem Effects of Fishing Activities. ICES CM 1996/Assess/Env:1.
- ICES. 1997. Report of the Multispecies Assessment Working Group. ICES CM 1997/Assess:16.
- Jones, R. 1982. Species interactions in the North Sea. Canadian Special Publication of Fisheries and Aquatic Sciences, 59: 48–63.
- Jones, R. 1984. Some observations on energy transfer through the North Sea and Georges Bank food webs. *Rapports et Procès-Verbaux des Réunion du Conseil International pour l'Exploration de la Mer*, 183: 204–217.
- Livingston, P.A., and Methot, R. 1998. Incorporation of predation into a population assessment model of eastern Bering Sea walleye pollock. Fishery stock assessment models of the 21st century. Alaska Sea Grant College Program Publication, AK-SG-98-01.
- MacArthur, R.H. 1970. Species packing and competitive equilibrium for many species. *Theoretical Population Biology*, 1: 1–11.
- MacArthur, R.H., and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. *American Naturalist*, 101: 377–385.
- MacCall, A.D. 1990. *Dynamic geography of marine fish populations*. University of Washington Press, Seattle, WA. 153 pp.
- May, R.M., Beddington, J.R., Clark, C.W., Holt, S.J., and Laws, R.M. 1979. Management of multispecies fisheries. *Science*, 405: 267–276.
- Menge, B.A., and Sutherland J.P. 1987. Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. *American Naturalist*, 130: 730–757.
- Mirza, F.B., and Gray, J.S. 1981. The fauna of benthic sediments from the organically enriched Oslofjord, Norway. *Journal of Experimental Marine Biology and Ecology*, 54: 181–207.
- Mommaerts, J.P., Pichot, G., Ozer, J., Adam, Y., and Baeyens, W. 1984. Nitrogen cycling and budget in Belgian coastal waters: North Sea areas with and without river inputs. *Rapports et Procès-Verbaux des Réunion du Conseil International pour l'Exploration de la Mer*, 183: 57–69.
- Murawski, S.A., and Idoine, J.S. 1992. Multispecies size composition: a conservative property of exploited fishery systems? *J. Northw. Atl. Fish. Sci.*, 14: 79–85.
- Murphy, E.J., and nine co-authors. 1998. Interannual variability in the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. *Fisheries Oceanography*, 7: 219–234.
- Paine, R.T. 1966. Foodweb complexity and species diversity. *American Naturalist*, 100: 65–75.
- Park, T. 1948. Experimental studies of interspecific competition. I. Competition between populations of the flour beetles *Tribolium confusum* Dival and *Tribolium castaneum* Herbst. *Ecological Monographs*, 18: 267–307.
- Park, T. 1954. Experimental studies of interspecific competition. II. Temperature, humidity and competition in two species of *Tribolium*. *Physiological Zoology*, 27: 177–238.
- Pascual, M., and Levin, S.A. 1999. From individuals to population densities: searching for the intermediate scale of nontrivial determinism. *Ecology*, 80: 2225–2236.
- Patrick, R. 1975. Structure of stream communities. In *Ecology and Evolution of Communities*, pp. 445–459. Ed. by M.L. Cody and J.M. Diamond. Belknap Harvard University Press, Cambridge, Massachusetts.
- Pianka, E.R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4: 53–74.
- Pianka, E.R. 1975. Niche relations of desert lizards. In *Ecology and Evolution of Communities*, pp. 292–314. Ed. by M.L. Cody and J.M. Diamond. Belknap Harvard University Press, Cambridge, Massachusetts.
- Pianka, E.R. 1983. *Evolutionary Biology*, 3rd Edition. Harper and Row, New York.
- Platt, T., and Denman, K. 1978. The structure of pelagic marine ecosystems. *Rapports et Procès-Verbaux des Réunion du Conseil International pour l'Exploration de la Mer*, 173: 60–65.
- Polovina, J.J. 1984. Model of a coral reef ecosystem I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs*, 3: 1–11.
- Pope, J.G., and Knights, B.J. 1982. Comparison of the length distributions of combined catches of all demersal fishes in surveys in the North Sea and at Faroe Bank. In *Multispecies approaches to fisheries management*, pp. 116–118. Ed. by M.C. Mercer. Can. Spec. Publ. Fish. Aquat. Sci., 59.

- Pope, J.G., Stokes, T.K., Murawski, S.A., and Idoine, S.I. 1988. A comparison of fish size composition in the North Sea and on Georges Bank. *In Ecodynamics: contributions to theoretical ecology*, pp. 146–152. Ed. by W. Wolff, C.J. Soeder, and F.R. Drepper.
- Rice, J., and Gislason, H. 1996. Changes in the abundance and diversity size spectra of the North Sea, as reflected in surveys and models. *ICES Journal of Marine Science*, 53: 1214–1225.
- Rijnsdorp, A.D., van Leewen, P.I., Daan, N., and Heessen, H.J.L. 1996. Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. *ICES Journal of Marine Science*, 53(6):1054–1062
- Rijnsdorp, A.D., and van Leewen, P.I. 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam trawl effort and temperature. *ICES Journal of Marine Science*, 53: 1199–1213.
- Rogers, S.I., Maxwell, D., Rijnsdorp, A.D., Damm, U., and Vanhee, W. In press. Comparing diversity of coastal demersal fish faunas in the northeast Atlantic. Fisheries Research.
- Rosenzweig, M.L. 1995. Species diversity in time and space. Cambridge University Press, UK. 436 pp.
- Rosenzweig, M.L., and Abramsky, Z. 1993. How are diversity and productivity related? *In Species diversity in ecological communities: historical and geographical perspective*, pp. 52–65. Ed. by R. Ricklefs and D. Schluter. University of Chicago Press, Chicago, Illinois.
- Ruardij, P., Barretta, J.W., and Barretta-Bekker, J.G. 1995. SESAME, a software environment for simulation and analysis of marine ecosystems. *Netherlands Journal of Sea Research*, 33: 261–270.
- Russo, A.R. 1982. Temporal changes in fish community structure near a sewage ocean outfall, Mokapu, Oahu, Hawaii. *Marine Environmental Research*, 6: 83–98.
- Sainsbury, K.J. 1991. Application of an experimental approach to management of a tropical multispecies fishery with highly uncertain dynamics. *ICES Marine Science Symposia*, 193: 310–320.
- Sanchez, F., and Olaso, I. 1999. Fisheries impacts in the Cantabrian Sea using a mass-balance model. *WGECO 1999/10*. 19 pp.
- Sheldon, R.W., Prakash, A., and Sutcliffe, W.H., Jr. 1972. The size distribution of particles in the ocean. *Limn. Oceanogr.*, 17: 337–340.
- Shin, Y.-J., and Cury, P. 1999. OSMOSE: a multispecies individual-based model to explore the functional role of biodiversity in marine ecosystems. Ecosystem considerations in fisheries management. Alaska Sea Grant College Program, AK-SG-99-01.
- Sparre, P. 1991. Introduction to multispecies virtual population analysis. *ICES Marine Science Symposia*, 193: 12–21.
- Spencer, P.D., and Collie, J.S. 1996. A simple predator-prey model of exploited marine fish populations incorporating alternative prey. *ICES Journal of Marine Science*, 53: 615–628.
- Steele, J.H. 1974. The structure of marine ecosystems. Blackwell, Oxford. 128 pp.
- Steele, J.H., and Henderson, E.W. 1981. A simple plankton model. *American Naturalist*, 117: 676–691.
- Stefánsson, G., and Pálsson, Ó.K. 1997. BORMICON. A Boreal Migration and Consumption Model. Marine Research Institute Report 58, Reykjavík. 223 pp.
- Thiebaut, M.L., and Dickie, L.M. 1993. Structure of the body-size spectrum of the biomass in aquatic ecosystems: a consequence of allometry in predator-prey interactions. *Can. J. Fish. Aquat. Sci.*, 50: 1308–1317.
- Tjelmeland, S., and Bogstad, B. 1998. Multispec—a review of multispecies modelling project for the Barents Sea. *Fisheries Research*, 37: 127–142.
- Tothmeresz, B. 1995. Comparison of different methods for diversity ordering. *Journal of Vegetation Science*, 6: 283–290.
- Vinter, M., and Thomsen, L. 1998. *Ad hoc* multispecies VPA tuning, an extension to 4M. ICES Study Group on Multispecies Model Implementation in the Baltic. Working Document 1998.
- Walters, C.J., Christensen, V., and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries*, 7: 139–172.
- Walters, C.J., Pauly, D., and Christensen, V. 1998. Ecospace: a prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *ICES CM 1998/S:4*. 22 pp.
- Walters, C.J., Stocker, M., Tyler, A.V., and Westreim, S.J. 1986. Interaction between Pacific cod (*Gadus macrocephalus*) and herring (*Clupea harengus pallasii*) in the Hecate Strait, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, 43: 830–837.

10 Testable Ecological Hypotheses About Fishing Effects

Having reviewed both empirical and model-based approaches to measuring impacts of fishing on ecosystem properties, the next step was to refine what hypotheses should be tested. WGECO considered it important that the evaluation of impacts be conducted, to the fullest extent possible, in a hypothesis testing framework, rather than just as an exercise in describing patterns in data or model results.

10.1 Development of Testable Hypotheses for Evaluating which Components of the Marine Ecosystem are Most Vulnerable to Trawl Impacts

WGECO was concerned with the apparent circularity in logic prevalent in the identification of vulnerable species. Rarely were such species proposed *a priori* on the basis of theoretical expectations. More commonly, vulnerable species were identified on the basis of their observed response to changes in fishing pressure. This circularity leads to uncertainty in the interpretation of data, and contributes to a degree of confusion regarding the value of particular species, or particular traits, as indicators of the impact of fishing on the ecosystem.

A more useful approach might be to first try to classify species on the basis of life history characteristics in a ranking order for vulnerability. Then one would test the hypothesis that those species which have been classified as the most vulnerable have actually shown a decline in response to fishing and vice versa. Such a classification should take place before any analysis of the data. Results could be taken a step further to address the question “can mean-values of specific characteristics of these populations, weighted by species abundance, be used to monitor the effects of fishing on the entire fish community?”.

A list of characteristics and traits for which it was thought there could be sound theoretical, or common sense, grounds for being able to predict a clear directional response to variation in fishing impact is developed below. The behaviour of as many of these characteristics and traits in some real data sets has been examined in Section 9.2, but will be tested formally in Section 10.4. Both spatial and temporal analyses were undertaken, looking for differences among areas differing in the level of fishing disturbance to which they have been subjected, and variation over time in areas where fishing impact has either increased or decreased. The analyses have been restricted to the potential impacts of fishing on fish species, and on trends in the mean characteristic value determined for the entire fish community or sub-components of it. A similar approach could be adopted for other components of the marine ecosystem, such as birds, marine mammals, invertebrates and benthic communities.

The effect of fishing on life history characteristics within a particular species is not considered here. (For example, does the age at maturity of individuals within a fished cod population decline?) This is another complex problem which, although of great interest, was beyond the scope of the WG to address in the time available.

10.2 Specific Hypotheses Regarding the Impact of Fishing on the Characteristics and Traits of Fish Communities

In this section many traits and characteristics of both species and fish communities are considered, *a priori* hypotheses are stated, and other initiatives are set out.

10.2.1 Specific hypotheses about populations and species abundances

When trying to characterise species based on life history characteristics there is extensive literature that distinguishes K-strategists from r-strategists on theoretical grounds and how their relative abundance in a community depends on the stability of their environment. This division is debatable and the categorisation of species into K- and r- strategists in this section is heuristic, and should not be interpreted as WGECO accepting the unqualified validity of this approach. Rather, the section explores how life history reasoning can be used in interpreting the results of studies of impacts of fishing. We ask, “Given the theoretical framework, can predictions of fishing effects be made and tested on a more *a priori* basis?”

According to this paradigm, K-strategists are adapted to living in stable and predictable environments and have greater competitive ability. They have longer life-spans, larger body size, reproduce later, produce few young, and are more likely to exhibit parental care. In contrast, r-strategists live in unpredictable or disturbed environments. They are small organisms with short life-spans, early reproduction and high fecundity. All gradations between the two extremes are possible and in practice it may be difficult to characterise a particular species as belonging to either strategy.

Therefore the approach chosen here was to use the values of life history parameters to indicate a species' position on the r/K continuum.

Fishing pressure increases mortality in all species. When this increase in mortality is placed in the context of life history theory it may have several consequences. Life history traits that change as a response to fishing will change in the same direction for all species, but the rates of change in the life history parameters should differ in important and informative ways. For a specific level of fishing mortality, populations of species with K-selected traits will decline faster than species with r-selected traits. Furthermore the life history characteristics will change faster for species at the K-end of the continuum. Thus the predicted responses by individual species to increased fishing disturbance are expressed below as testable hypotheses relative to what would be expected for r-selected species:

- Species with large ultimate body length (L_{max} or L_{inf}) should decline;
- Species with slow growth rates (e.g., k from the von Bertalanffy equation) should decline;
- Species with older age at maturity (A_{mat}) should decline;
- Species with longer length at maturity (L_{mat}) should decline;
- Species with a low fecundity and lower life-time reproductive output should decline.

For a given level of fishing mortality, at the community scale the percentage of the community composed of species with K-selected traits will decline. Because of responses predicted for individual species, the response of each of these characteristics calculated across the assemblage as a whole is predictable. The community average character values, weighted by species abundance, should respond to an increase in fishing disturbance as follows:

- | | |
|---------------------------------|----------|
| • L_{max} | Decrease |
| • L_{inf} | Decrease |
| • Growth Rate | Increase |
| • Fecundity | Increase |
| • Life-time reproductive output | Increase |
| • A_{mat} | Decrease |
| • L_{mat} | Decrease |

These changes in growth rate and fecundity should affect the productivity of the fish assemblage. Thus:

- The overall production to biomass (P/B) ratio of the fish community should be higher in more intensively fished areas, and it should increase as fishing disturbance increases.

The trophic level at which fish feed is strongly size dependent; larger fish in the community tend to be piscivores, smaller fish are planktivores and/or benthivores. With the decline of larger fish in more heavily fished areas, or as fishing in an area increases, the trophic structure of the community should change (e.g., Pauly *et al.*, 2001).

- Species that feed at higher trophic level will be more sensitive and should decline as fishing effort increases, or have a lower abundance in heavily fished areas.
- The average trophic level of the fish community should decline as fishing intensity increases, and be lower in more heavily fished regions.

Because of an increase in the amount of damaged and killed benthic organisms left lying on the seabed as a consequence of demersal fishing, species best able to utilise this resource are likely to increase in abundance.

- The proportion of fish that can be considered scavengers should have increased in intensively fished areas.

Species with obligate habitat requirements should decline in abundance when such habitat is lost as a consequence of fishing activity.

- Species that depend on a three-dimensional habitat (e.g., a fragile biogenic habitat) should decline in abundance and have a lower abundance in areas where habitat is altered by increased levels of trawling.

WGECO 2000 suggested that species richness should decline more in intensively fished areas than in less disturbed areas. This can be tested in two ways:

- Spatially, species richness should be lower in areas of high fishing intensity;
- Temporally, species richness should decline in areas where fishing intensity is increasing.

Many factors could confuse the response of species diversity to changes in fishing levels. Huston's (1994) dynamic equilibrium model suggests that the response of species diversity to disturbance is dependent upon local productivity.

- Species diversity should decline in response to increased fishing disturbance in areas of low productivity. In areas of high productivity, increased fishing could cause species diversity to increase.

Fish also pass through the meshes of the gear and can become damaged in the process, which could increase mortality and susceptibility to disease.

- The prevalence of fish showing sub-lethal effects (scarring, scale loss, external lesions, etc.) in intensively fished areas should be higher compared with fish in relatively undisturbed regions.
- Species which are particularly sensitive to the effects of scale loss, etc., are likely to decline in abundance as fishing intensity increases, and to have lower abundance in areas of high fishing activity, relative to insensitive species.

10.2.2 Spatial Hypotheses

Many attributes of the two- and three-dimensional distribution of species or groups of species have not been well explored. This section attempts to develop some spatial metrics and apply them in a provisional way to fisheries survey data. In Atlantic Canada two metrics of distribution are commonly reported in single-species assessments: the area covered by a species and an index of concentration, which is the area containing the densest portion of the resource (Branton and Black, 2000).

The proposed metrics are applicable to single-species and are aggregated into community or group indices. It is not clear, or perhaps even likely, that the aggregated indices will be more valuable than those for specific single-species. As the work is exploratory it is offered as a stimulus to further work as opposed to a definitive or prescriptive study.

There is an implicit hypothesis that the distribution of animals may affect their viability and further that some species will be more sensitive to displacement than others. Further if species are perturbed, their community may also be affected. For example, if they are scattered too widely, they may be subject to higher predation or compromised recruitment. Conversely, if they are concentrated into a small area, they could suffer increased fishing mortality per unit effort (Paloheimo-Dickie effect (Paloheimo and Dickie, 1964)). Another consideration is displacement from traditional spawning areas. It is further assumed that fishing activity (or pollution) could affect these distributions. At this time hypotheses about which species or species groups will be most affected have not been posed.

10.3 Approach

The analysis performed by WGECCO had two purposes:

Firstly, to use the most comprehensive data available to test a set of specific hypotheses with the purpose of identifying those characteristics and traits of fish species and communities that might be most useful as metrics of trawling impact. This required three basic types of information:

- 1) Trawl survey data providing information on the species' abundance in samples of fish. These data must extend over sufficient time so as to have substantial contrast in fishing events if the hypotheses being tested involve the evaluation of temporal trends. Alternatively, if the tests involve spatial comparisons, a reasonably large and dynamic geographic range is required.
- 2) Information on species characteristics or traits, for example, age at maturity, or habitat requirements of the species caught in the trawl surveys. Such information is required for a sufficient number of species so as to ensure that a reasonably large fraction of the total number of individuals caught in each sample are included.
- 3) Information on the variation in fishing effort, over time and/or space, is necessary for directly testing hypotheses. Ideally the temporal and/or spatial extent of the data should match that/those of the groundfish survey data.

Secondly, to explore the potential use of these metrics as indicators of impending ecological problems for managers. Thus temporal and spatial trends in the abundance of potentially sensitive species were explored, as well as trends in the metrics calculated for the entire fish community in an area where fishing effort data were not available. The reasoning behind this analysis was to explore whether the fish community concerned was affected by fishing activity in the area.

10.4 Analysis of the Data Sets

10.4.1 Northwest North Sea (Scottish August groundfish surveys)

In this section we use Scottish August Groundfish Survey (SAGFS) data, international and Scottish fishing effort data, and information on life history characteristics of the species encountered in the survey data, to test some specific hypotheses derived from the theoretical expectations presented in Section 10.2. A primary objective of the section is to identify which, if any, of the life history parameters examined might hold potential as a metric of fishing-induced change in the fish community, and the particular circumstances where the greatest insight might be gained. The data

presented cover 75 ICES statistical rectangles located in the northwestern North Sea where data coverage is most reliable (Figure 10.4.1.1).

10.4.1.1 Species characteristics

Information regarding four life history characteristics (L_{inf} , Growth Rates, A_{mat} , L_{mat}) was available for 32 of the species (Jennings *et al.*, 1998, 1999a) encountered in the SAGFS, listed in Table 10.4.1.1.1. The L_{inf} and Growth Rate were the parameter values determined from the von Bertalanffy growth equation calculated for each species. The von Bertalanffy parameter is not strictly a rate value, but is used here as an index equivalent to growth rates. A_{mat} and L_{mat} values were determined by observation, either from recent survey data or with recourse to the literature. These 32 species accounted for over 99% of the individuals sampled by the SAGFS in each of the 75 statistical rectangles. No life history characteristic information was available for the remaining 24 species included in the database. These species were among the rarest sampled, and combined they represented less than 1% of the total number of individuals sampled in any rectangle. Their influence on the mean value of each characteristic could only have been negligible. For the purposes of this analysis, therefore, abundance data for these species were excluded. In the final temporal analysis, the proportion of the sampled fish assemblage in any time-period/"treatment" cell never dropped below 98.5%.

10.4.1.2 Effort

International otter trawl, beam trawl, and Seine net fishing effort (hours fished) for the period 1990 to 1995 were available from the database compiled as part of the EC "Monitoring Biodiversity..." project (Jennings *et al.*, 1999b, 2000). Average annual effort values were calculated to provide estimates of the spatial distribution of fishing effort across the 75 ICES statistical rectangles for which groundfish survey data were available. Total annual average fishing effort across the 75 statistical rectangles amounted to 963 216 hours of fishing, 67% of which consisted of otter trawling, 12% beam trawling, and 21% Seine netting.

The possibility that the life history composition of the groundfish assemblage was affected not only by the absolute amount of fishing effort in any statistical rectangle, but also by recent trends, was also considered. The international fishing effort database covered only the years 1990 to 1995 and so does not provide much of a time-series. The Scottish fishing effort database extends further back in time (Greenstreet *et al.*, 1999b). Furthermore, Scottish vessels landing in Scotland account for most of the fishing effort in this part of the North Sea. Indices of annual rates of change in otter trawl, beam trawl, and Seine net effort were therefore determined for each of the 75 statistical rectangles using the Scottish data. Effort data for Seine net and otter trawl were available for the period 1970 to 1994 for each rectangle. Average annual effort for the five-year periods 1970 to 1974 and 1990 to 1994 were computed for both gears. The difference between these values was divided by 20 to provide average annual rates of change for each gear in each rectangle over the 25-year period. Beam trawling is a relatively recent phenomenon in the northwestern North Sea, and effort data for this gear were only recorded from 1984 onwards. The same approach described above was adopted, except that the start point five-year period was 1984 to 1989, and the divisor was 5, thus providing an annual rate of change in beam trawl use index over a ten-year period.

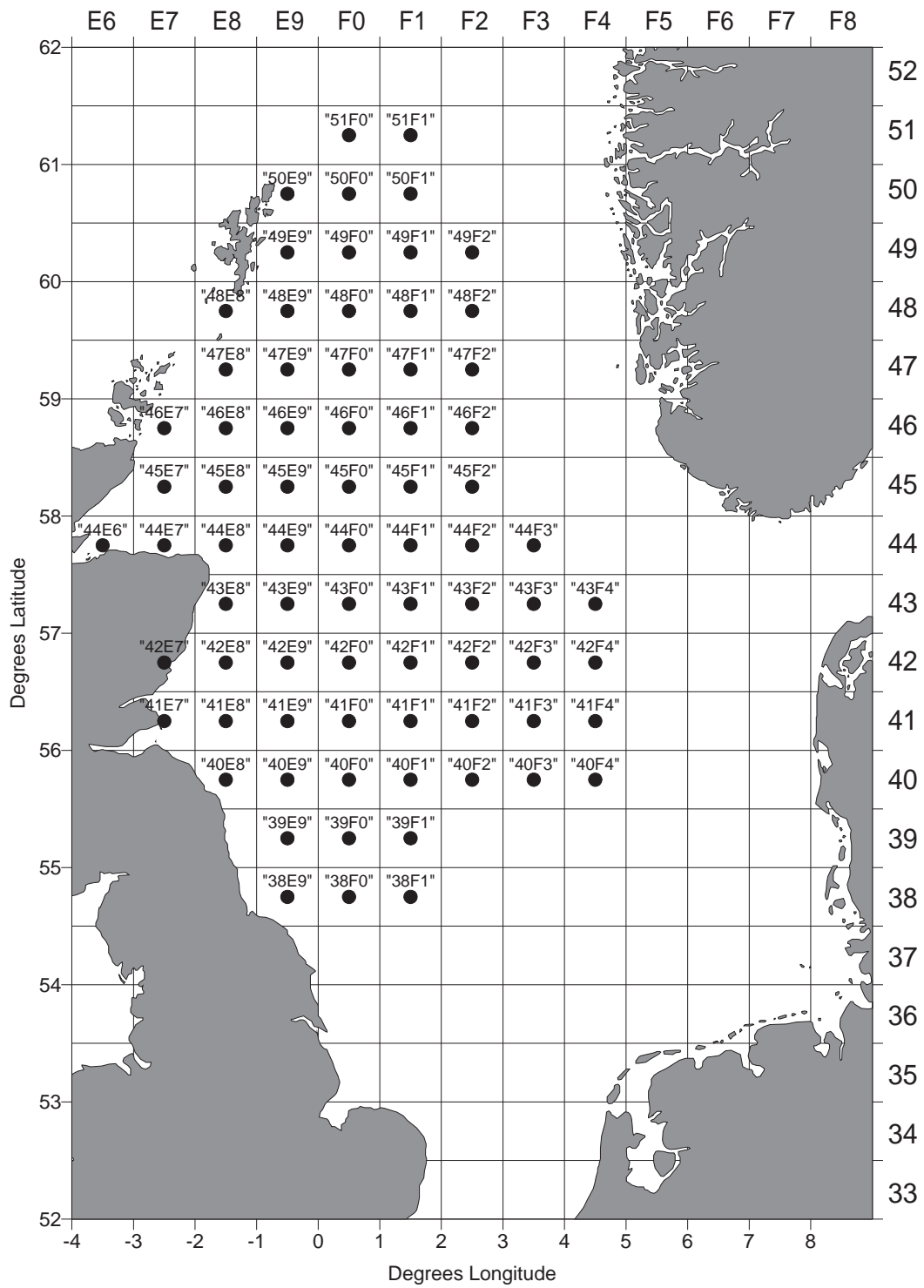


Figure 10.4.1.1 Area of the North Sea covered by the data sets analysed in this section.

Table 10.4.1.1.1 List of species encountered in the SAGFS for which life history character information was available.

Angler	<i>Lophius piscatorius</i>
Bull rout	<i>Myoxocephalus scorpius</i>
Catfish	<i>Anarhichas lupus</i>
Cod	<i>Gadus morhua</i>
Common dab	<i>Limanda limanda</i>
Cuckoo ray	<i>Raja naevus</i>
Dover sole	<i>Solea solea</i>
Dragonet	<i>Callionymus lyra</i>
Four-bearded rockling	<i>Enchelyopus cimbrius</i>
Grey gurnard	<i>Eutrigla gurnardus</i>
Haddock	<i>Melanogrammus aeglefinus</i>
Hake	<i>Merluccius merluccius</i>
Halibut	<i>Hippoglossus hippoglossus</i>
Hooknose	<i>Agonus cataphractus</i>
Lemon sole	<i>Microstomus kitt</i>
Lesser spotted dogfish	<i>Scyliorhinus canicula</i>
Long rough dab	<i>Hippoglossoides platessoides</i>
Megrim	<i>Lepidorhombus whiffiagonis</i>
Norway pout	<i>Trisopterus esmarki</i>
Plaice	<i>Pleuronectes platessa</i>
Poor cod	<i>Trisopterus minutus</i>
Saithe	<i>Pollachius virens</i>
Skate	<i>Raja batis</i>
Spotted ray	<i>Raja montagui</i>
Spurdog	<i>Squalus acanthias</i>
Starry ray	<i>Raja radiata</i>
Thornback ray	<i>Raja clavata</i>
Three-bearded rockling	<i>Gaidropsarus vulgaris</i>
Torsk	<i>Brosme brosme</i>
Turbot	<i>Scophthalmus maximus</i>
Whiting	<i>Merlangius merlangus</i>
Witch	<i>Glyptocephalus cynoglossus</i>

10.4.1.3 Survey (catch) data

Groundfish survey data collected as part of the Scottish August Groundfish Surveys were examined. Trawl species abundance data were extracted for 75 ICES statistical rectangles in the northwestern North Sea covering a period of 14 years from 1983 to 1996. Up to four trawl samples were then excluded as necessary in order to reduce the number of samples to 10 in all rectangles. For one rectangle, data for the years 1983, 1985, 1987 and 1995 were missing. In reducing the number of trawls to 10 in the remaining rectangles, samples from these years were selected and deleted at random as required. All ten trawl samples in each rectangle were then pooled to provide a single aggregated sample for each rectangle. The samples for each rectangle were thus standardised as far as possible, given the type of sampling involved. All trawl samples were collected by the FRV “Scotia (II)”, using a 48-foot Aberdeen otter trawl, towed for one hour (Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999a). The number of trawl samples per rectangle was the same for all rectangles, thus avoiding any sample-size dependency issues.

Species abundance data were converted to the number of individuals with particular characteristic values, and the mean value for each characteristic for each rectangle was computed. Data were available only for groundfish species likely to be well sampled by the gear. Pelagic species and other species not well sampled by the 48-ft Aberdeen otter trawl, such as herring, sprat, and sandeels, were all excluded from the data set. The results therefore only apply to the demersal groundfish community occupying the area.

For the final analysis, looking at long-term temporal trends in rectangles varying in the level of fishing effort to which they had been subjected, data from the full time-series were used. As in Greenstreet *et al.* (1999b) data were pooled into groups of two or three years to ensure adequate sampling effort in each time-period/“treatment” cell.

10.4.1.4 Analysis and results

This section is hypothesis driven. A series of specific hypotheses are presented, all of which are related to or derived from the theoretical discussion presented in Section 10.2. The data are then analysed so as to test each hypothesis.

Hypothesis: Groundfish assemblage Growth Rates should be positively correlated, and L_{inf} , L_{mat} and A_{mat} should be negatively correlated in space, with fishing effort.

Life history characteristic data were plotted against international effort data. Relationships between assemblage average life-history characteristics and otter trawl and beam trawl effort in each of the 75 statistical rectangles were similar. Also, since otter trawl effort exceeded beam trawl effort by a factor of six, data for both gears were aggregated. The effects of the two gears combined on each of the life history characteristics were then examined (Figure 10.4.1.4.1). Correlation coefficients were computed and used as a guide to identify life history characteristics that could potentially be useful as metrics indicative of an effect of fishing on groundfish communities. All four life history characteristics responded to increased trawling effort in a manner predicted by our hypothesis; however, only the correlations for A_{mat} and L_{mat} were significant at the 5% level. Furthermore, some caution is required in interpreting the significance of any of the correlations presented in this section, since the degrees of freedom applied take no account of the fact that these are essentially spatial analyses. Because of the strong possibility of spatial auto-correlation between many of the data points used, rendering them not truly independent of each other, the actual number of degrees of freedom is likely to be less than, in this case, 73.

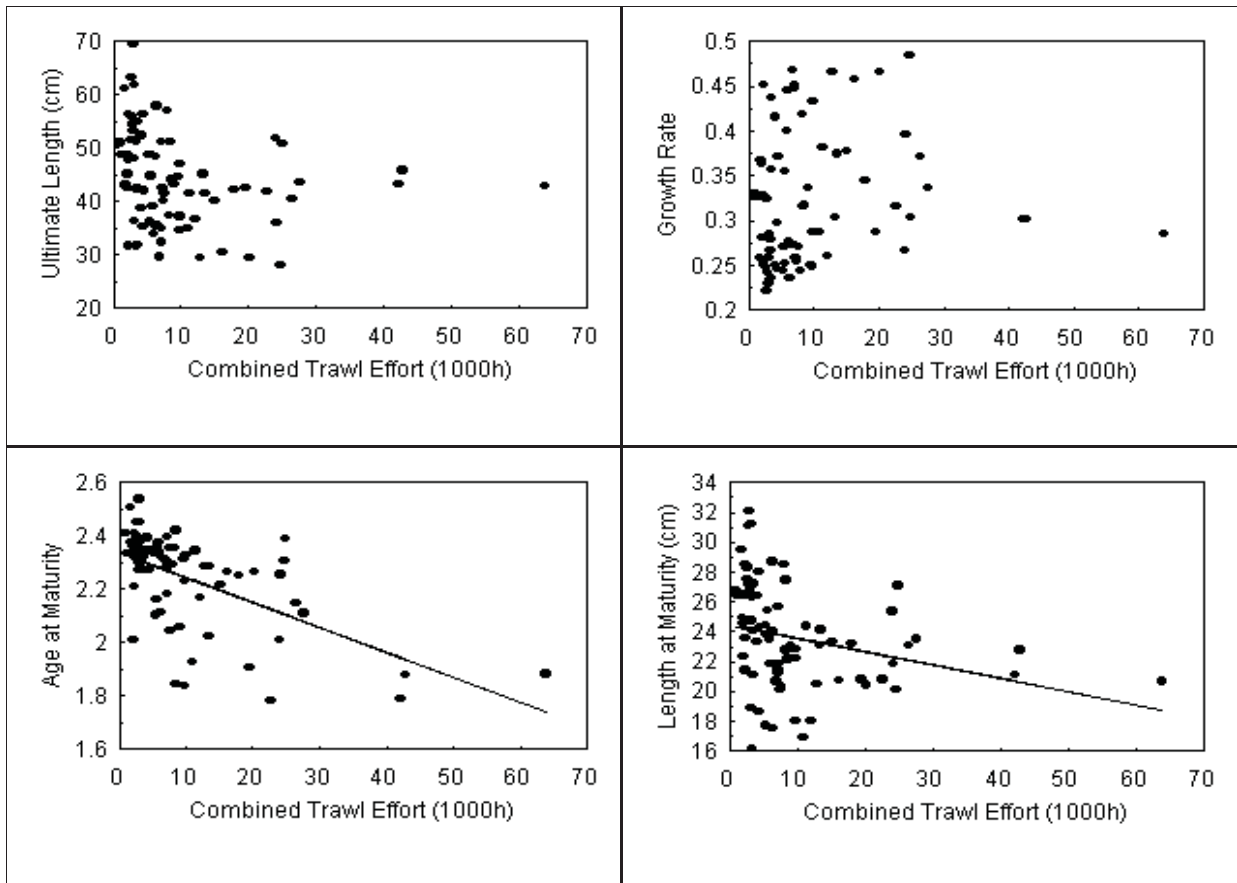


Figure 10.4.1.4.1 Relationship between combined otter and beam trawl effort in 75 ICES statistical rectangles and the average and $Length_{\infty}$, Growth Rate, $Age_{Maturity}$ and $Length_{Maturity}$ determined for 32 species making up >99% of the total number of individuals sampled in each rectangle.

By the early 1990s, use of Seine net gear in this part of the North Sea had declined from the high levels characteristic of the 1960s. Nevertheless, the relationship between spatial variation in Seine net effort and the life history characters of the groundfish assemblage in each statistical rectangle was also explored (Figure 10.4.1.4.2). Three characters were correlated at the 5% level of significance: Growth Rate, A_{mat} and L_{mat} . However, only the relationship for Growth Rate was in the direction predicted by our hypothesis. Seine net used to be the predominant type of gear used in a large part of the northwestern North Sea. Over recent decades this gear has largely been replaced by otter trawls. It is possible that the relationships displayed in Figure 10.4.1.4.2 have been influenced by this change in fishing practice, such that the relationships between any character and Seine net use have been affected by the impact of otter trawling in the same rectangles.

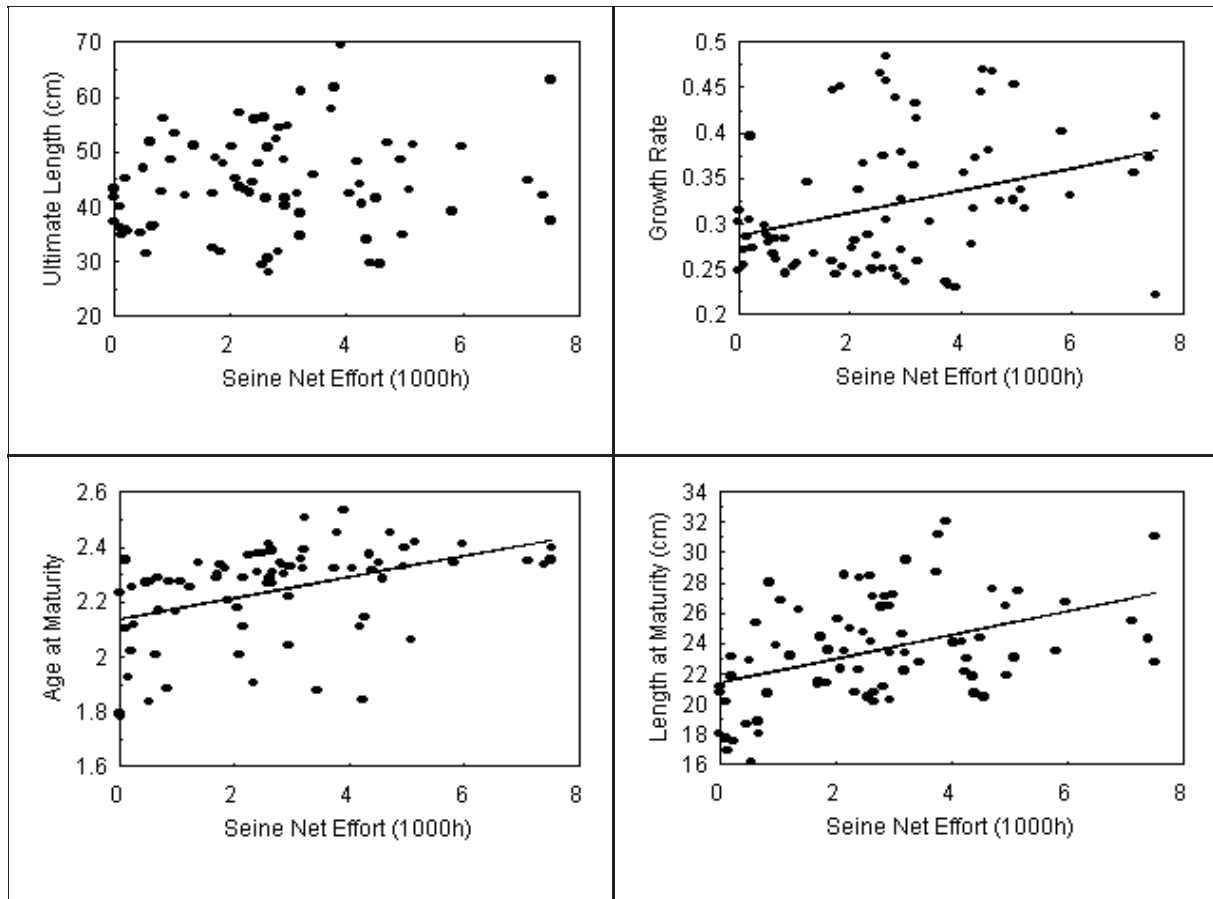


Figure 10.4.1.4.2. Relationship between Seine net effort in 75 ICES statistical rectangles and the average and $Length_{Infinity}$, Growth Rate, $Age_{Maturity}$ and $Length_{Maturity}$ determined for 32 species making up >99% of the total number of individuals sampled in each rectangle.

Hypothesis: Groundfish assemblage Growth Rates should be positively correlated, and L_{inf} , L_{mat} and A_{mat} should be negatively correlated in space with rates of change in fishing effort over recent years.

Relationships between mean assemblage life history characteristics and annual rates of change in fishing effort in each rectangle were examined (Figure 10.4.1.4.3). The correlations for the L_{inf} and Growth Rate were significant at the 5% level, whilst those for A_{mat} and L_{mat} were not. These two sets of results raise the possibility that assemblage mean L_{mat} and A_{mat} might provide indicators of the effect of absolute levels of fishing effort on the life history composition of the groundfish communities, while mean L_{inf} and Growth Rate could reflect recent changes in fishing effort. However, a small number of points have very high leverage in these calculations, so patterns must be viewed with extra caution.

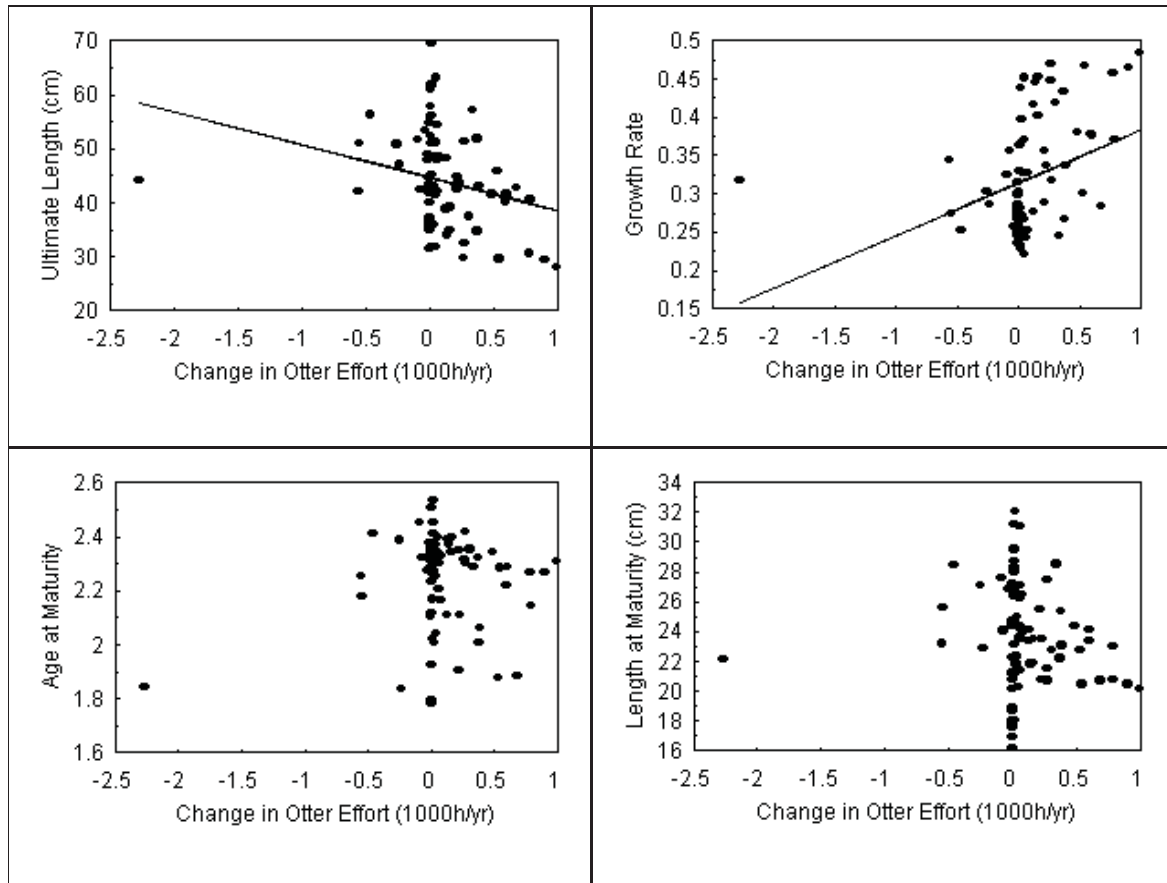


Figure 10.4.1.4.3 Relationship between annual average rate of change in otter trawl effort in 75 ICES statistical rectangles over the period 1970–1994 and the average and L_{inf} , Growth Rate, A_{mat} and L_{mat} determined for 32 species making up >99% of the total number of individuals sampled in each rectangle.

Hypothesis: Groundfish assemblage Growth Rates should be higher, and L_{inf} , L_{mat} and A_{mat} should be lower in areas with higher fishing effort.

Levels of international otter trawl fishing effort ranged from 645 hr yr⁻¹ to 63 794 hr yr⁻¹ across the 75 ICES statistical rectangles. The rectangles were sorted into three groups varying in the intensity to which they had been fished during the early 1990s: a low-intensity group of 40 rectangles where effort varied from 0 to 4999 hr yr⁻¹; a medium-intensity group of 25 rectangles in which effort varied from 5000 to 19 999 hr yr⁻¹; and a heavily fished group of 10 rectangles in which effort exceeded 20 000 hr yr⁻¹. The mean, and standard error of the mean, of each life history characteristic was determined for each group of rectangles (Figure 10.4.1.4.4). Differences, tested using one-way ANOVA, were found to be significant at the 1% level for all four characteristics. In each case, the trend was consistent with the hypothesis.

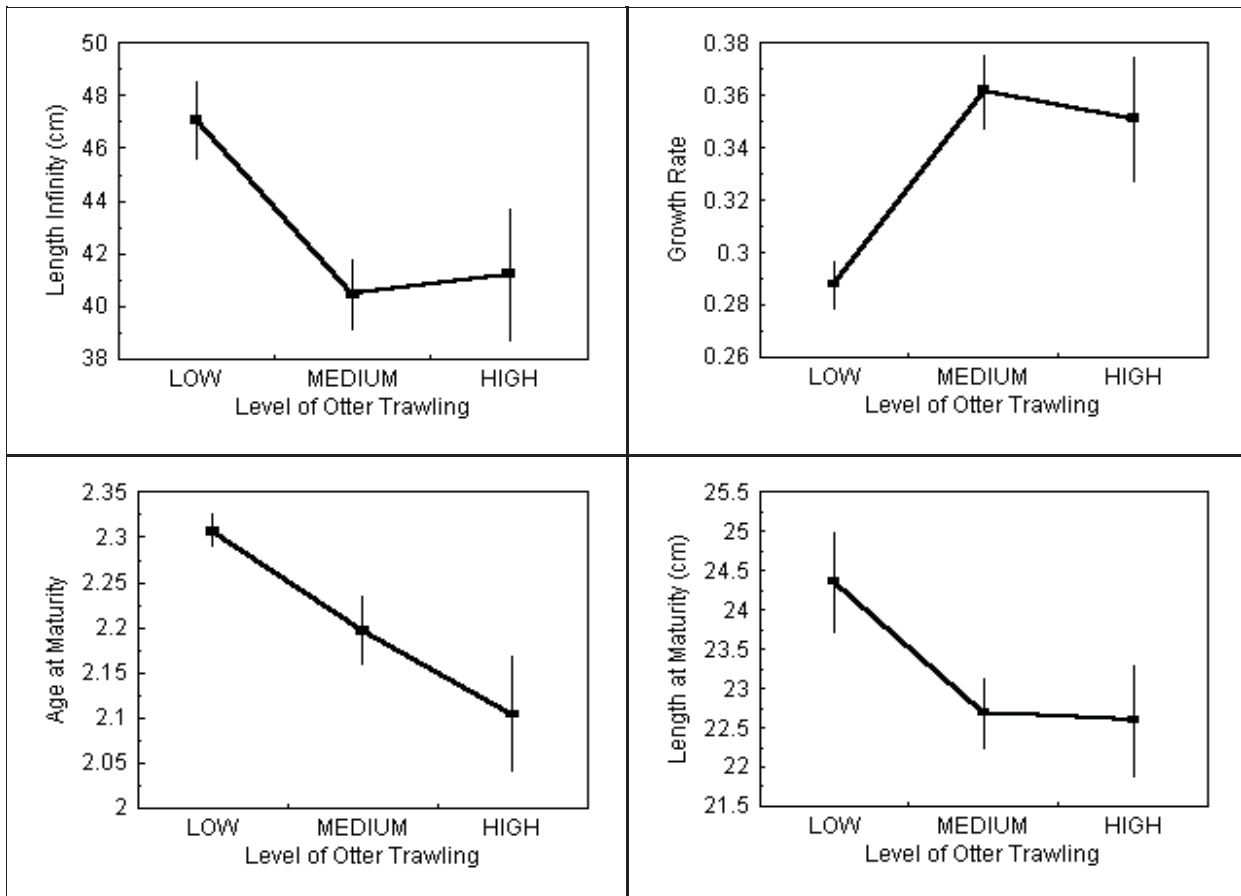


Figure 10.4.1.4.4 Variation in the mean (± 1 S.E.) L_{inf} , Growth Rate, A_{mat} and L_{mat} determined for 32 species making up >99% of the total number of individuals sampled in each rectangle calculated for groups of rectangles varying in the level of otter trawl effort to which they were subjected.

L_{inf} , Growth Rates and L_{mat} appeared to be the most sensitive characteristics, differentiating most between low and medium fishing intensity groups of rectangles. Beyond a certain level (threshold?) of perturbation, variation in these characteristics tended to level out. This raises the possibility that, as metrics, these three characteristics may be relatively insensitive in already disturbed areas. On the other hand, A_{mat} continued to decrease strongly as otter trawl effort increased from low, through medium, to high levels.

Hypothesis: Groundfish assemblage Growth Rates should be higher, and L_{inf} , L_{mat} and A_{mat} should be lower in areas where fishing effort is increasing at the greatest rate.

Annual rates of change in otter trawl effort varied from the extreme outlier of -2268 hr yr^{-1} to 991 hr yr^{-1} . Three groups of rectangles were again defined: a group of 19 rectangles where otter trawl effort was declining; a group of 35 rectangles where effort was increasing slowly, between 0 and 199 hr yr^{-1} ; and a group of 21 rectangles where effort was increasing rapidly, between 200 and 991 hr yr^{-1} . The mean, and standard error of the mean, of each life history characteristic was determined for each group of rectangles (Figure 10.4.1.4.5). Differences, tested using one-way ANOVA, were found to be significant at the 1% level for all four characteristics. Only the Growth Rate behaved entirely as anticipated by the hypothesis. For the three remaining characteristics, the highest mean parameter values were observed on the rectangles with slow rates of increase in otter trawl effort.

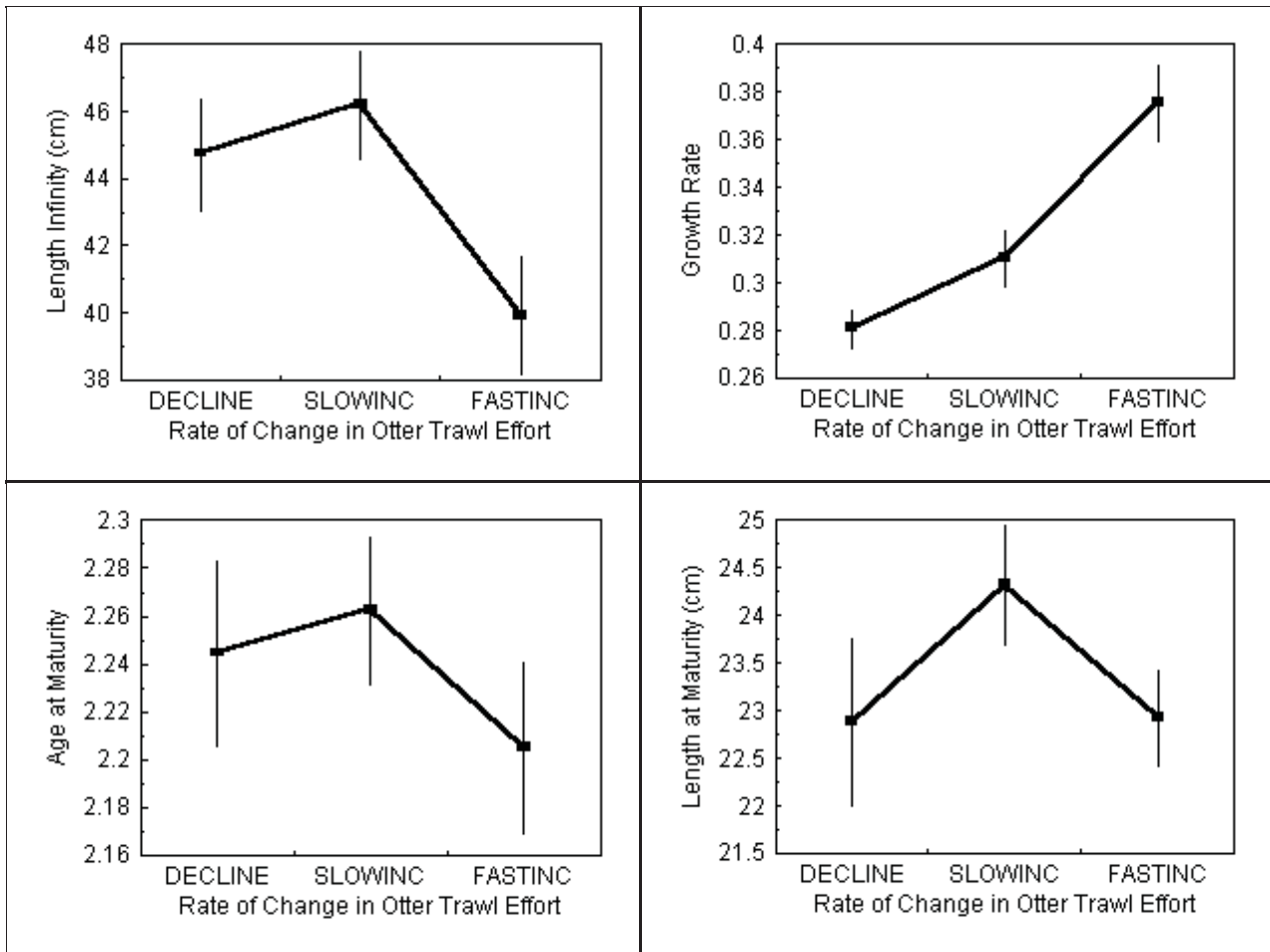


Figure 10.4.1.4.5. Variation in the mean (± 1 S.E.) L_{inf} , Growth Rate, A_{mat} and L_{mat} determined for 32 species making up >99% of the total number of individuals sampled in each rectangle in groups of rectangles with different annual rates of change in otter trawl effort.

Hypothesis: Long-term temporal variation in groundfish assemblage Growth Rates should show steeper positive trends, and L_{inf} , L_{mat} and A_{mat} steeper negative trends, in areas where fishing effort is higher, and in areas where recent trends in fishing effort have shown the greatest rates of increase.

This analysis used the full time-series of available groundfish survey data, from 1925 to 1996, to explore the long-term behaviour of community mean life history characteristics in areas of varying fishing intensity. The rectangles were grouped into the same three treatment levels of international otter trawl effort during the early 1990s, and for recent trends in Scottish otter trawl effort over the period 1970 to 1994. As before, abundance-weighted mean character values for the groundfish community were determined for each time/treatment cell. These were then regressed over time and the regression coefficients (± 1 S.E. of the coefficient) were plotted for each treatment and life history characteristic (Figures 10.4.1.4.6 and 10.4.1.4.7).

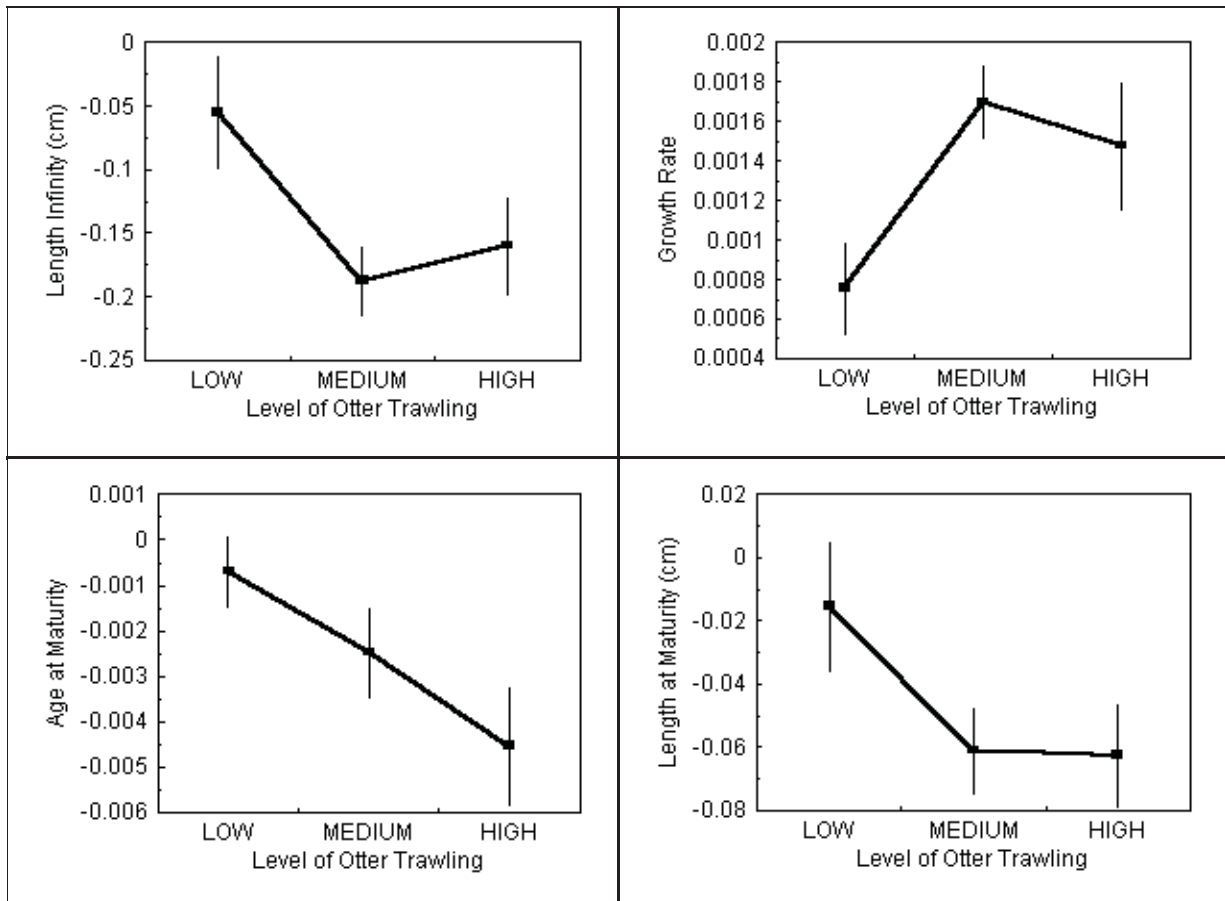


Figure 10.4.1.4.6 Variation in the regression coefficients (± 1 S.E. of the coefficient) for the slopes of L_{inf} , Growth Rate, A_{mat} and L_{mat} over the time period 1925 to 1995 in rectangles with different mean levels of annual international otter trawl effort over the period 1990 to 1995.

All four parameters showed very little change in rectangles where levels of otter trawl impact were low. Indeed, none of the long-term regression analyses were significant. However, in rectangles with medium and high levels of international otter trawl effort during the early 1990s, all the long-term trends were significant, and in the direction predicted by our hypotheses (Figure 10.4.1.4.6). Of interest again was the fact that L_{inf} , Growth Rate and L_{mat} all failed to differentiate between medium and high levels of fishing effort. Again, this suggests that these parameters may be able to distinguish between fished and unfished areas, but once an area is impacted, they may be relatively insensitive to further perturbation. A_{mat} , however, showed increasingly steep long-term declines as otter trawl effort increased from medium to high levels of otter trawl activity. This analysis therefore again suggests that this index may hold the greatest promise as a metric able to provide managers with an ongoing indication of the continuing effect of their actions on the life history composition of the groundfish community.

The data presented in Figure 10.4.1.4.6 are also helpful in aiding our interpretation of Figure 10.4.1.4.4 as they suggest that the current community-averaged life history parameters (e.g., Figure 10.4.1.4.4) are the result of long-term changes from some earlier common, presumably near pristine, state.

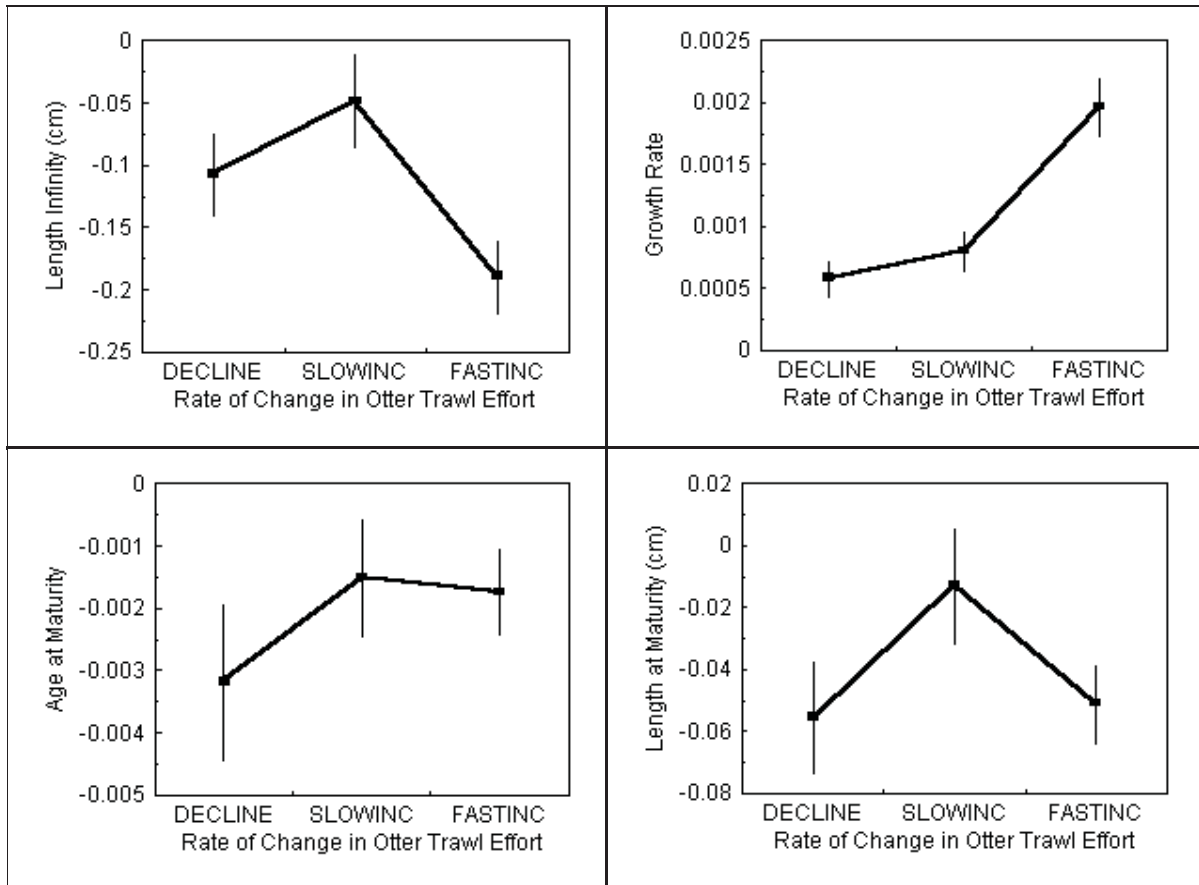


Figure 10.4.1.4.7 Variation in the regression coefficients (± 1 S.E. of the coefficient) for the slopes of $Length_{\infty}$, Growth Rate, $Age_{Maturity}$ and $Length_{Maturity}$ over the time period 1925 to 1995 in rectangles with different annual rates of change in Scottish otter trawl effort over the period 1970 to 1994.

As with Figure 10.4.1.4.5, the interpretation of Figure 10.4.1.4.7 is more problematic. For example, Figure 10.4.1.4.7 suggests that the greatest long-term rates of decline in both A_{mat} and L_{mat} occurred in rectangles where otter trawl activity has actually declined over the period 1970 to 1994. This clearly contravenes the hypothesis. L_{mat} does show steeper long-term declines in rectangles where otter trawling has increased most rapidly over the period 1970 to 1994. A_{mat} fails even to do this. Variation in L_{inf} and Growth Rate, however, both support the hypothesis. The long-term decline in L_{inf} and long-term increase in Growth Rate are both steepest in the rectangles where otter trawling has increased most rapidly over the period 1970 to 1994.

Hypothesis: Species richness should be lower in areas where current levels of fishing effort are highest, and in areas where recent trends in fishing effort have shown the greatest increase.

Species richness was determined for each of the statistical rectangles from simple counts of all the different species recorded in each rectangle. Mean species richness was determined for three groups of rectangles with low (0 to 4999 hr yr⁻¹), medium (5000 to 19 999 hr yr⁻¹), and high levels (>20 000 hr yr⁻¹) of fishing intensity. The same approach was adopted for examining the effect of trends in fishing effort over a 25-year period. Three groups of rectangles were defined, characterised by their annual rates of change in otter trawl effort: a group where otter trawl effort was declining; a group where effort was slowly increasing, between 0 and 199 hr yr⁻¹; and a group where effort was increasing rapidly, between 200 and 991 hr yr⁻¹. In both cases, differences between the groups were examined by one-way ANOVA (Figure 10.4.1.4.8). In each case, significant variation was detected, but in the direction opposite to that predicted by the hypothesis. Either fishing has caused an increase in species richness, or fishing has increased most in areas where species richness is highest.

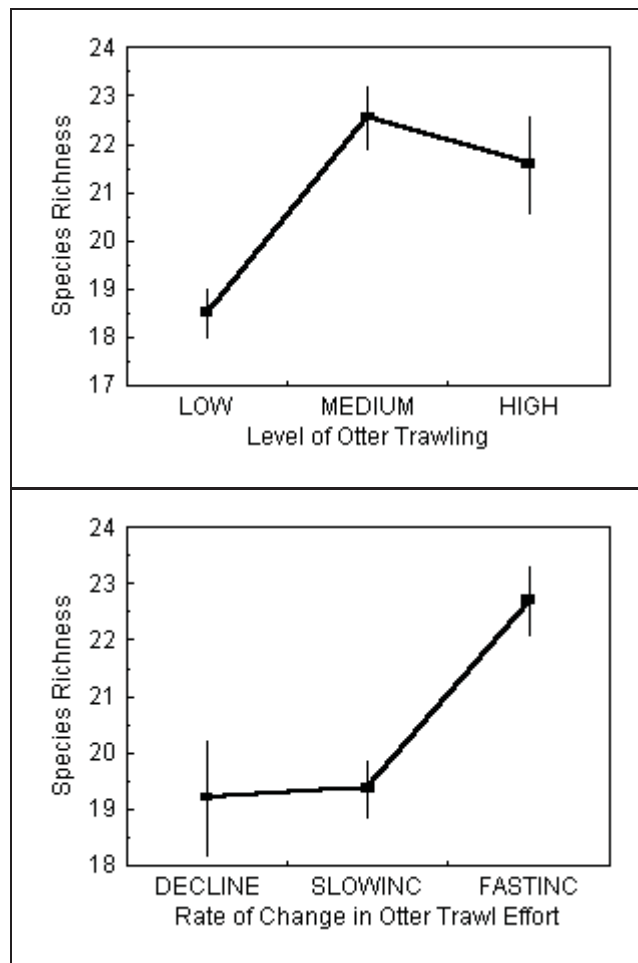


Figure 10.4.1.4.8 Variation in mean species richness (\pm 1 S.E.) calculated for groups of rectangles varying in the level of otter trawling to which they were subjected between 1990 and 1995, and in which the annual rates of change in otter trawling differed over the period 1970 to 1994.

Hypothesis: Species diversity should be lower in areas where current levels of fishing effort are highest, and in areas where recent trends in fishing effort have shown the greatest increase.

The same treatments and analyses applied to examine the relationship between otter trawling and species richness were applied to two species diversity indices calculated from the pooled species abundance data for each of the 75 statistical rectangles. All ANOVAs were significant ($P < 0.01$). In this instance, the responses of species diversity to variation in fishing effort lay in the anticipated direction. The difference in species diversity between areas of medium and high otter trawling intensity was marginal. However, both indices appeared to be sensitive to the full range of annual rates of change in fishing activity (see Figure 10.4.1.4.9).

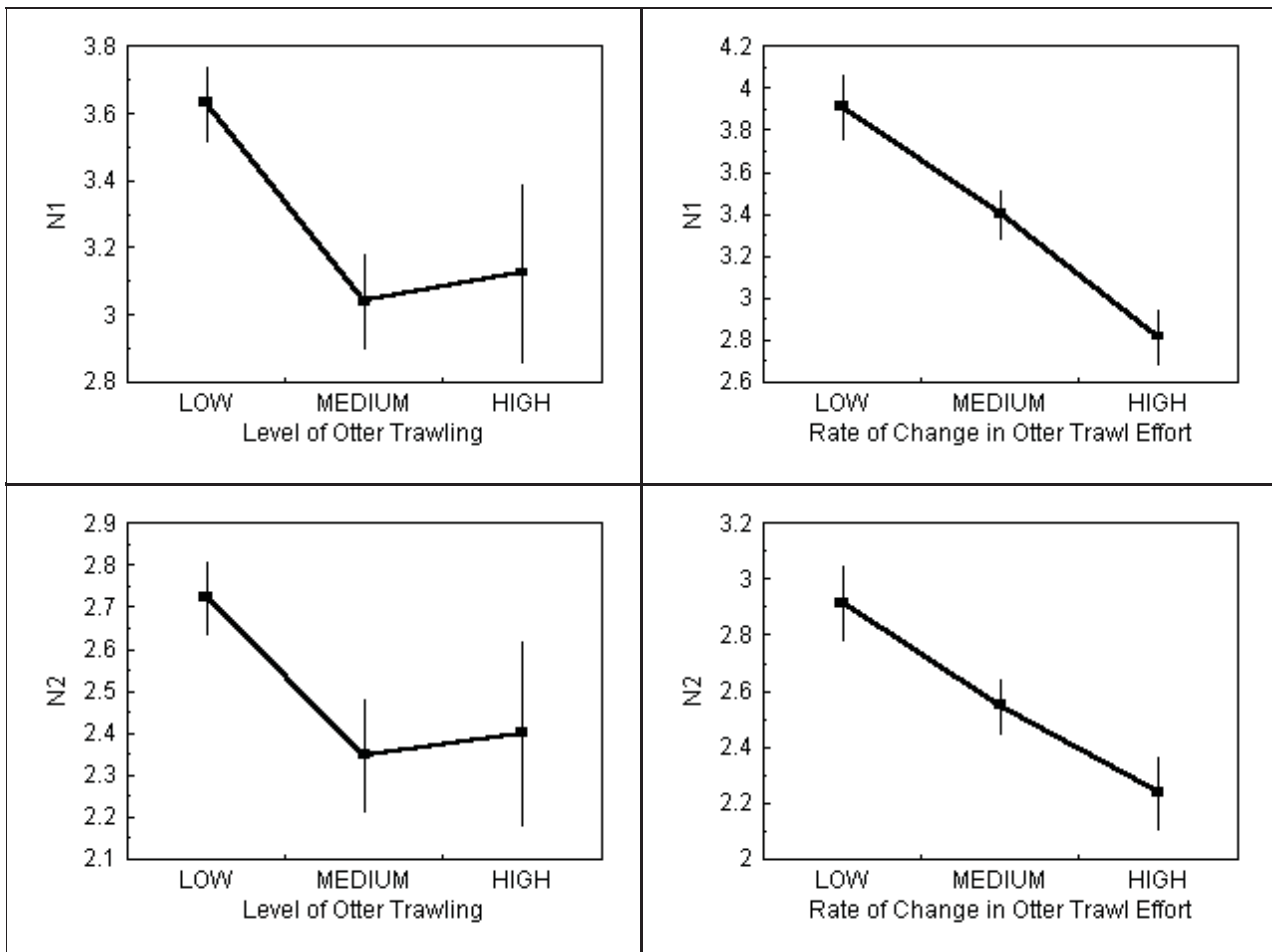


Figure 10.4.1.4.9 Variation in mean species diversity N1 and N2 (± 1 S.E.) calculated for groups of rectangles varying in the level of otter trawling to which they were subjected between 1990 and 1995, and in which the annual rates of change in otter trawling differed over the period 1970 to 1994.

10.4.1.5 Summary of Scottish AGFS results and conclusions

Table 10.4.1.5.1 summarises the results obtained in the analyses carried out on the northwestern North Sea Scottish August Groundfish Survey data. These results clearly demonstrate that mean life history characteristics can detect effects of trawling. Again these results seem to suggest, as emphasised by WGECCO in the past, that the application of a suite of metrics provides more information than any single metric alone. This is particularly true for the North Sea where fishing levels are high. Several of the life history characteristics appeared particularly sensitive to the effects of fishing at low fishing intensity. Under some circumstances, these metrics may not detect any further change in impact once otter trawl effort exceeds 5000 hr yr^{-1} .

The results for the two Hill's (1973) diversity indices, N1 and N2, appeared to detect the effect of variation in fishing effort on species relative abundance in the groundfish community. They seemed particularly sensitive to changing levels of fishing disturbance. These data tend to corroborate the previous analyses of this data set. The response of species richness to variation in fishing impact was entirely contrary to the predictions of the hypothesis.

Does fishing cause an increase in species richness? An alternative explanation is that fish abundance has increased most rapidly, and is now at high levels, in areas where species richness is greatest. This highlights the shortcoming of all analyses of this type—they are still not controlled experiments. However, more detailed analysis of this data set, taking account of other sources of variation, such as depth and other environmental factors, may still provide further insight into true cause and effect.

Table 10.4.1.5.1 Summary of results on Scottish AGFS data set (- no analysis, ✓ indicates a significant result, ✗ indicates result was non-significant, footnotes provide further commentary, LTb = slope of the long-term time-series).

Independent variable or treatment	Dependent variable or measure	Analysis	Parameter						
			L _{inf}	k	A _{mat}	L _{mat}	S	N1	N2
Effort level	Parameter	Correlation	✗	✗	✓	✓	-	-	-
Rate of change effort	Parameter	Correlation	✓	✓	✗	✗	-	-	-
Effort level	Mean parameter	ANOVA	✓ ₁	✓ ₁	✓	✓ ₁	✓ ₃	✓ ₁	✓ ₁
Rate of change effort	Mean parameter	ANOVA	✓ ₂	✓	✓ ₂	✓ ₃	✓ ₃	✓	✓
Effort level	Parameter LTb	ANOVA	✓ ₁	✓ ₁	✓	✓ ₁	-	-	-
Rate of change effort	Parameter LTb	ANOVA	✓ ₂	✓	✓ ₃	✓ ₃	-	-	-

Cell entries are used to summarize patterns as:

- 1) Most differentiation was between low and medium levels of fishing effort. Data suggest either a threshold or a strongly non-linear effect. If used as a metric it may detect the effect of trawling impact as effort increases from low levels, but may not detect variation in impact as effort varies in relatively heavily fished areas.
- 2) Could be classed as insensitive—only differentiated between those rectangles where rates of change in effort varied from slow to fast increase. No difference between areas of slow increase and areas of decline in effort.
- 3) Significant ANOVA, but results difficult to interpret with respect to the hypothesis.

10.4.2 North Sea IBTS data

10.4.2.1 Species characteristics

A table of life history characteristics of fish species caught in the International Bottom Trawl Survey (IBTS) was modified from Daan (2001). Only a few of the life history characteristics could be obtained for the majority of the 266 species; these are maximum length, biogeographical area, habitat, lifestyle, and trophic level. For species with no maximum length (L_{max}) reported for the North Sea, the global value reported for that species was used. Habitat refers primarily to the water depth where the fish is found (e.g., shelf, slope), whereas lifestyle refers to where in the water column the fish is found (e.g., demersal, pelagic). Of these two, habitat was considered most useful for testing the above hypotheses. Trophic level was extracted from FishBase (www.fishbase.org) where it has been calculated from diet information or ECOPATH analyses of the ecosystems in which the given species live.

Additional life history characteristics that were recorded for a subset of the species include maximum age, age and length at maturity, L_{inf} and K from the von Bertalanffy equation, fecundity and egg size. However, these parametric estimates were only available for the subset of the species that are routinely sampled for age.

Ideally, each species could be ranked on an r/K continuum. One measure of the rate of increase (r) is the productivity parameter (∞) from a stock-recruitment relationship. Stock-recruitment relationships can be calculated for commercially important species for which SPAs are available, but not for the entire set of species found in the trawl surveys. Hall and Collie (unpublished) found an inverse relationship between the Ricker ∞ and L_{inf} . In this study L_{max} is used as an approximation for L_{inf} . In this manner, L_{max} is a surrogate for the rate of increase; species with low L_{max} are at the r end of the r/K continuum and vice versa, as is expected.

10.4.2.2 Survey data

For the North Sea the hypotheses regarding the effects of fishing on traits of the fish community were tested using the International Bottom Trawl Survey (IBTS) data. The IBTS is a follow-up of the International Young Fish Surveys (IYFS) that were conducted in the North Sea and Skagerrak/Kattegat in February of each year starting in the late 1960s. Over the years, the survey has changed from a survey on young herring into one for demersal fish and herring of all ages and sizes. At the same time, the area surveyed has expanded until from 1974 onwards the whole North Sea proper, Skagerrak, and Kattegat were covered. The IBTS was conducted in international collaboration, with different research

vessels covering specific areas. Over time standardization in gear type, rigging specifications, and sampling strategy was carried out by participating countries (ICES, 1999). During the early years of the survey, a 78-foot Dutch herring trawl was recommended as the standard gear, but in 1977 it was decided to use the GOV-trawl (Grande Ouverture Verticale) as standard gear. From then onward most vessels used GOV, but it took several years before it was adopted by all vessels. The GOV has a high vertical net opening of 5 to 6 m. The horizontal opening of the net is approximately 20 m. Standard fishing speed is 4 knots measured as trawl speed over the ground. Each haul lasts 30 minutes. For the present study, only quarter 1 data from the North Sea proper (excluding the Kattegat and Skagerrak) were used for the years 1974 until present. Each year only those hauls were used where all species caught were recorded.

10.4.2.3 Analysis and results

The hypothesis tested was that “species whose maximum length recorded in the entirety of any particular data set (L_{max}) should decline”.

To assess the effect that life history strategy may have on the (changes in) abundance of populations, a life history index was developed based on a species’ maximum length by weighting the biomass per species in the annual IBTS catch with the maximum length as expressed in Piet (2001). The average maximum length was shown to decrease significantly ($p < 0.01$) from about 41 cm at the start of the sampling period to about 38 cm at the end of that period (Figure 10.4.2.3.1), indicating a relative increase of r-selected species.

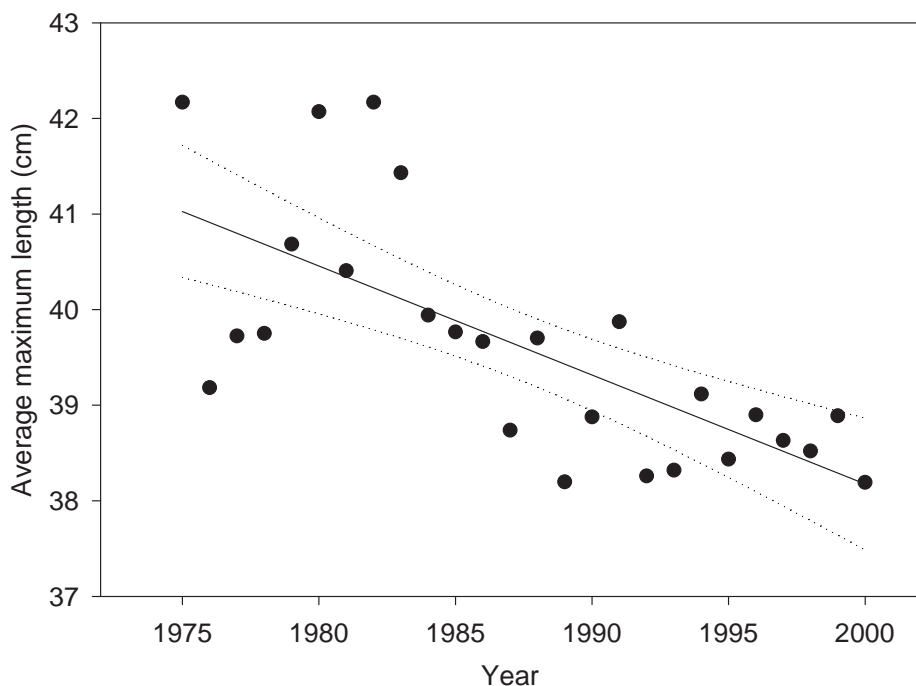


Figure 10.4.2.3.1. Average maximum length of the fish community over time. Points are values per year, lines show fit and 95% confidence interval.

The effect of fishing effort on the maximum length index was studied by determining the mean maximum length and slope of the change in the maximum length index over time per ICES rectangle and combining these with the effort data per ICES rectangle according to Jennings *et al.* (1999a, 1999b, 2000).

The mean maximum length showed a significant ($p < 0.01$) decrease with fishing effort. Combination of ICES rectangles into three effort-classes (Low $\leq 10\,000$, $10\,000 < \text{Medium} \leq 30\,000$, High $> 30\,000 \text{ hr yr}^{-1}$) showed a significantly higher mean maximum length for ICES rectangles where fishing effort was “Low” (Figure 10.4.2.3.2).

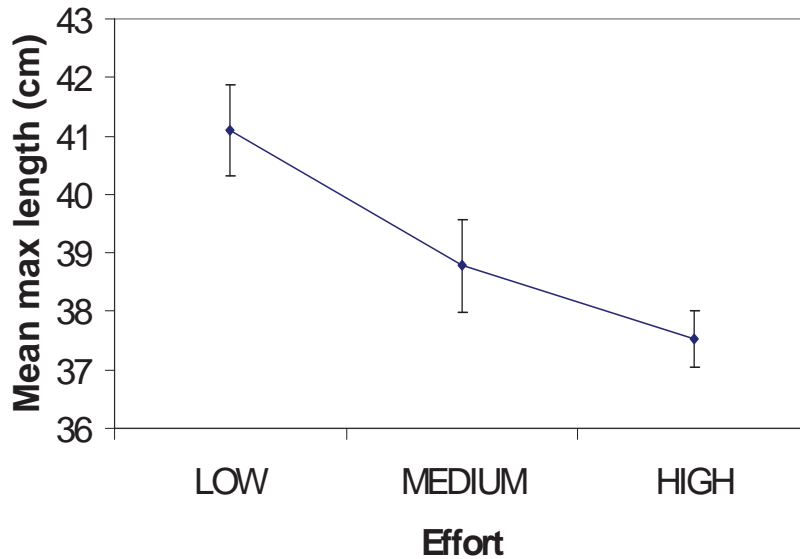


Figure 10.4.2.3.2 Mean Length_{max} and 95% confidence limits for three classes of fishing effort (Low≤10 000, 10 000<Medium≤30 000, High>30 000 hr yr⁻¹). Based on 161 ICES rectangles for which IBTS and effort data were available.

The slope of the change in maximum length over time in relation to fishing effort is shown in Figure 10.4.2.3.3. Slope did not decrease with increasing effort as might be expected. The reason is that a significant inverse relationship between mean maximum length and slope was observed. This suggests that in the heavily fished ICES rectangles the composition of the fish community in terms of life history traits has stabilized at a relatively high level of r-strategists represented by a low mean maximum length.

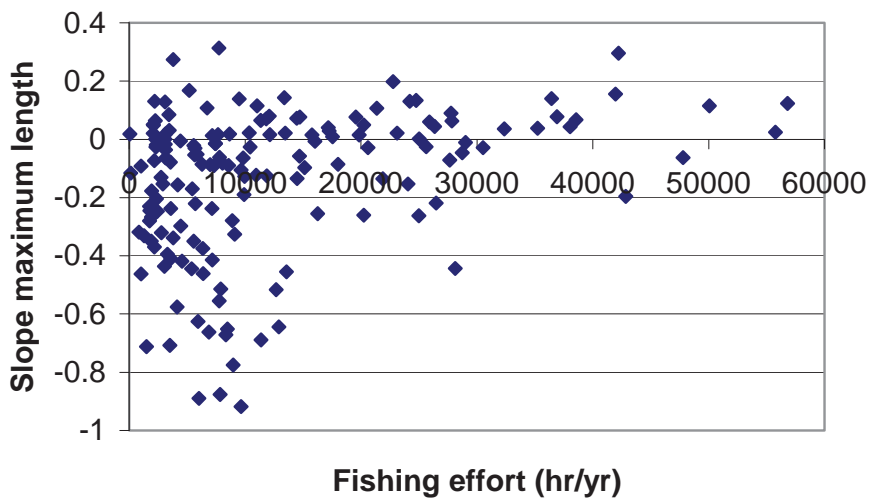


Figure 10.4.2.3.3 Relationship between the slope of the mean maximum length over time and fishing effort in 161 ICES rectangles.

10.4.3 Portuguese survey data

10.4.3.1 Species characteristics

Life history characteristics for 194 species caught in the Portuguese demersal survey were compiled by the Working Group. Of this group of species, 105 were common to the North Sea. An effort was made to standardize the sets of life history categories between regions such that these categories would be applicable to all regions of the North Atlantic. As for the North Sea, the variables that were available for most of the species were L_{max} , lifestyle, habitat and trophic level. These life history characteristics are global values for the species (extracted from FishBase, Whitehead *et al.*, 1984) and were not collected as part of the trawl survey. The 38 species for which one or more species characteristic were missing were excluded from the data set. These were all very rare species, collectively representing only 0.057% of the total number of all individuals in the data set.

10.4.3.2 Survey data

Demersal survey cruises have been carried out annually in continental Portuguese waters since 1979 and are well described in Cardador *et al.* (1997) (Figure 10.4.3.2.1). Data from the autumn (fourth quarter) surveys for 1982 and from 1989 to 2000 are used here. All stations are separated into three geographical zones (North, Centre and South) at 39.5 °N and 37.1 °N latitude, and into two depth strata (less than and more than 150 m). This gave six groups of data that were used for all subsequent analyses. The criteria for these choices were largely taken from Gomes *et al.* (2001). For each year and for each of these groups, the total number of individuals of each species (after being scaled up to number of individuals for 1 hour for each haul, when necessary) was determined.

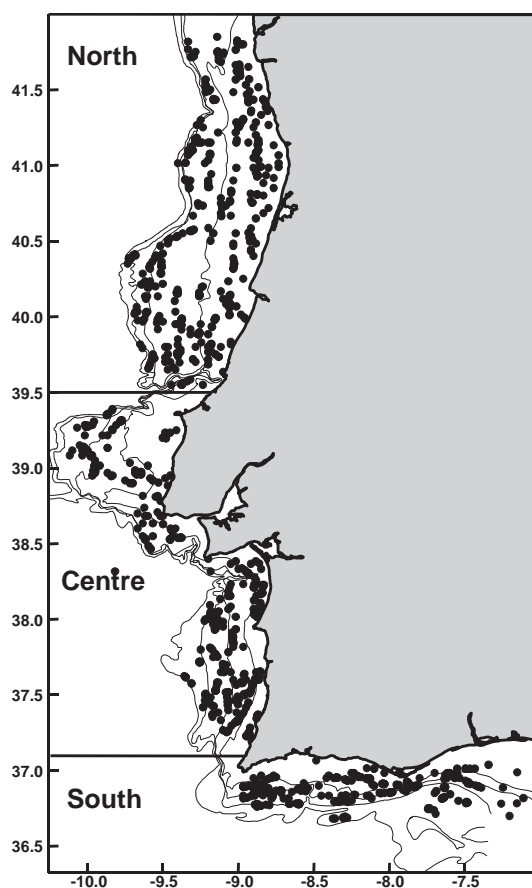


Figure 10.4.3.2.1 Map of continental Portuguese waters, showing survey stations (•), the three geographical zones (North, Centre and South) and with 100, 200, 500 and 750 m contour lines.

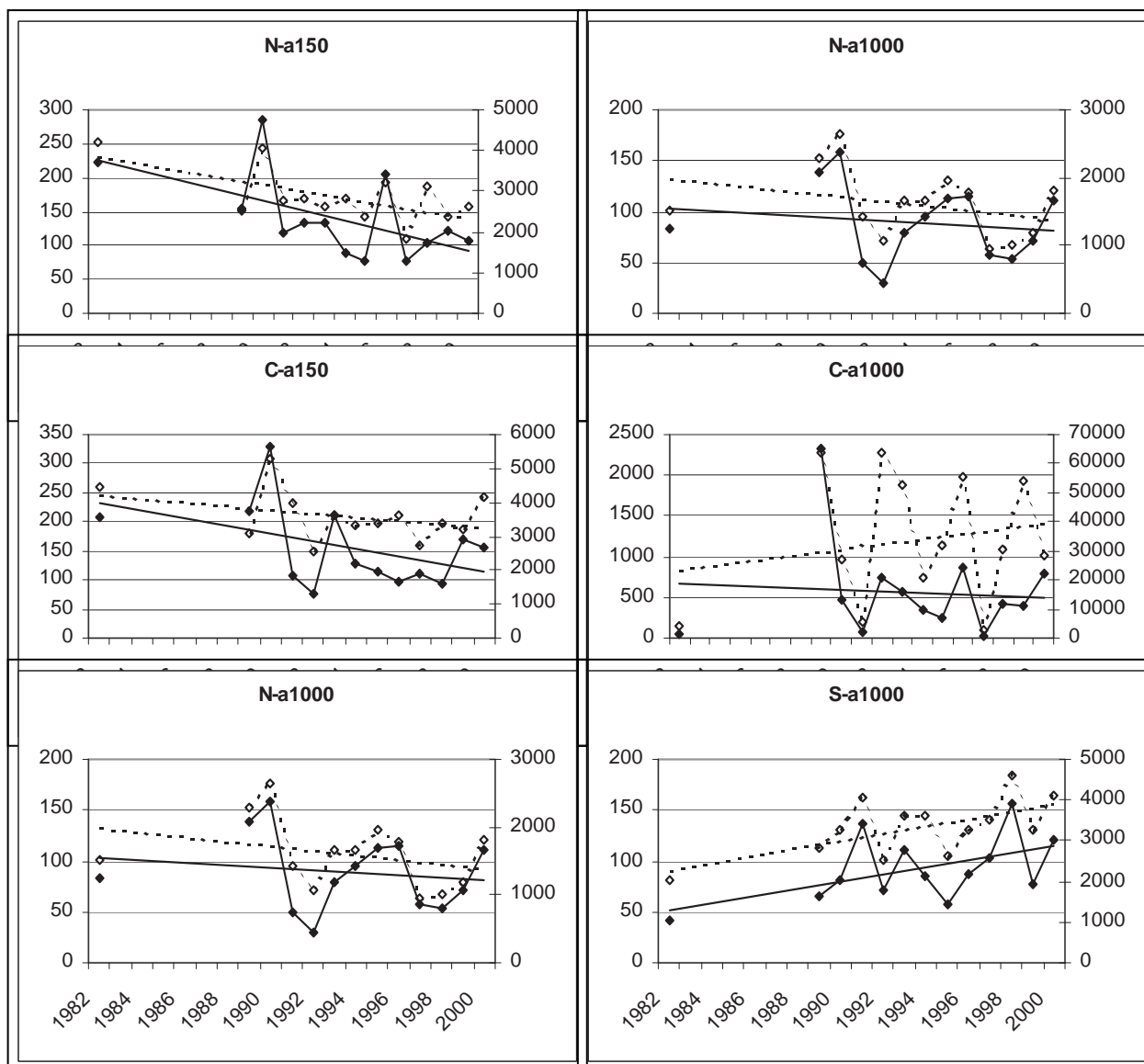
10.4.3.3 L_{max} and trophic level analysis and results

In order to test the hypotheses about L_{max} and trophic level presented above, the trends in these characteristics over time were analysed. This was done by calculating the weighted average value for each year based on the biomass of each species and the individual species characteristic value. These values were then plotted against time and trend lines

determined (Table 10.4.3.3.1, Figure 10.4.3.3.1). From these data the following trends were observed, as shown in Figure 10.4.3.3.1.

Table 10.4.3.3.1 Trends (\Downarrow = decrease, \Uparrow = increase) in weighted averages of L_{max} and trophic level. Values are R^2 , a decrease with an R^2 over 0.25 is significant).

	L_{max}	Trophic level
North shallow	\Downarrow 0.335	\Downarrow 0.402
North deep	\Downarrow 0.022	\Downarrow 0.096
Centre shallow	\Downarrow 0.203	\Downarrow 0.130
Centre deep	\Downarrow 0.006	\Uparrow 0.036
South shallow	\Uparrow 0.137	\Uparrow 0.090



South deep	\Uparrow 0.278	\Uparrow 0.407
------------	------------------	------------------

Figure 10.4.3.3.1 Plots of weighted averages of L_{max} and trophic level for 6 groups (N=North, C=Centre, S=South; a150=1–150 m, a1000=151 to 1000 m). Solid lines for L_{max} , dashed lines for trophic level.

It can therefore be seen that, except for in the north shallow group, these data do not show a significant decrease. There are a number of potential explanations for this, which could include:

- A decrease in exploitation since 1982;
- A change in faunal composition due to immigration of new species;
- The fishery targets small species;
- The shortness of the time-series.

It is not surprising that there are differences between the north groups and the others as there are strong physical differences between these zones. The north has a relatively large and flat continental shelf. The northern and central zones are divided by the Nazaré canyon, and below this point the shelf is considerably more narrow.

These analyses strongly suggest that these metrics are not reliable indicators on their own, at least not in this system. The life history traits are changing, but the patterns of change usually are not as predicted by theory, and the reasons for the changes are not understood. For example, in the centre deep group L_{max} decreased while trophic level increased. Both data sets contain a lot of noise, but trophic level more so, suggesting that trophic level is a less sensitive metric. Whether the differences between the results of these analyses and those using the Scottish data (Section 4.4.1), where a number of life history parameters were thought to have changed in ways consistent with theory, are due to differences between the ecosystems, between the fisheries, or just due to the differences in contrast within the data sets, remains to be explored.

10.4.3.4 Spatial metrics analysis

10.4.3.4.1 Description of data

The data were selected from the Portuguese survey data. Only data for elasmobranchs (27 species) and gadids (13 species from the Gadidae family) were used in order to keep the set small, but providing some contrast. Because of their reproductive strategies, elasmobranchs *a priori* may be expected to be more susceptible to effort. The distribution of the survey is shown in Figure 10.4.3.4.1. The subset had year, longitude-latitude, depth, species name, numbers caught, biomass caught, L_{max} and trophic level. The time-series was for 1982 and 1989–2000. Preparatory to the analysis the data were aggregated to a tenth of a degree squares and a code number given to each species to aid analysis. It would have been beneficial to apply the following analyses to other data sets, but time constraints prohibited this. In the following, we use the term community to denote either the elasmobranch or the gadoid group.

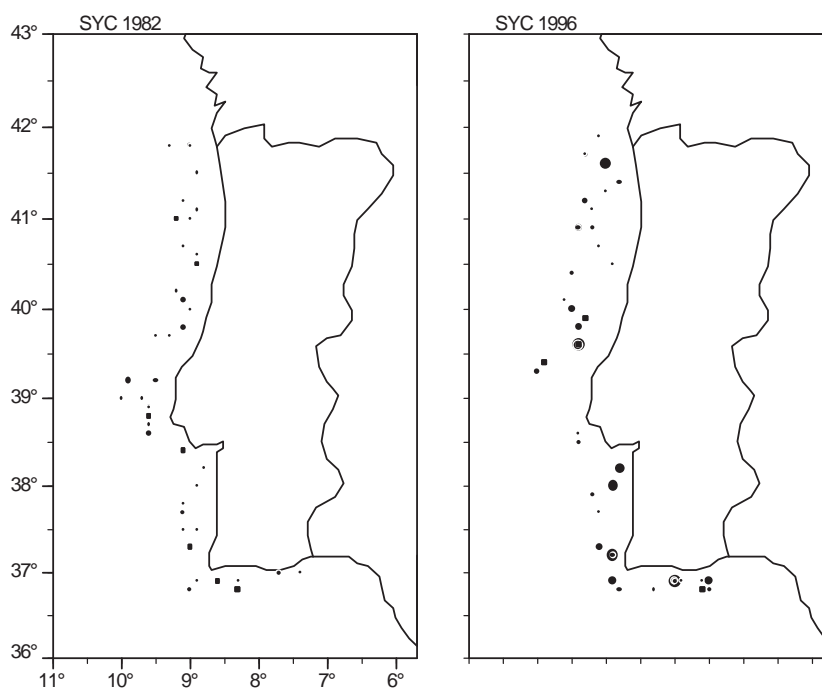


Figure 10.4.3.4.1 Sample data from the Portuguese survey series. The figure contains the aggregated biomass for *Scyliorhinus canicula* 1982 and 1996. Larger circles reflect higher abundance.

Unfortunately, the data available (a subset of the Portuguese trawl survey) did not have sufficient quality (duration and knowledge of, or dynamic range of, effort) to test the effect of fishing effort on the metrics. Instead of a hypothesis-based study, a preliminary investigation of the performance of three spatial metrics on a single data set is reported.

10.4.3.4.2 Description of metrics

Because of the unavailability of effort data, the metrics were compared to abundance trends over the time-series. Both the unweighted biomass per tow and L_{\max} weighted biomass were considered.

Spatial metric 1 – Anomaly of the center of mass of the community.

Based on experience from Eastern Scotian Shelf cod, a metric was proposed which is the anomaly of the centre of mass of distribution. In that case it was noted that the centre of mass seemed to predict a subsequent rapid decrease in biomass in the late 1980s. The metric is calculated by first computing the centre of mass for each year and summing over the species or community under consideration. The average over time-series of centroids is found and then the distance (in nautical miles) from each annual point to the average is found giving an annual anomaly.

Spatial metric 2 – Index of contagion

A contagion index is proposed which is the number of neighbours within a set radius. Figure 10.4.3.4.2.1 shows three different distributions of four animals or sets of animals and a test radius of 2 units. In the upper plot, the four animals are so far apart that they have no neighbours within the test radius. In the middle plot, the four animals are in a row and there are three pairs of neighbours within the radius. Finally in the bottom plot, all four animals are in a cluster and the index is now 6. Because it is hypothesised above that contagion is probably more important on the species level, this metric is computed for each species of concern and then summed for all species under consideration. This sum could either be unweighted or weighted by abundance.

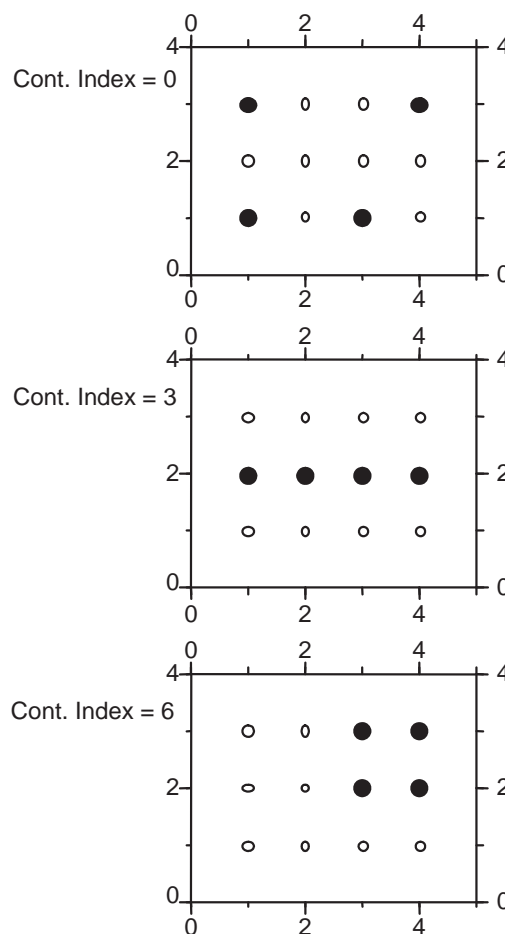


Figure 10.4.3.4.2.1 Samples of contagion index.

Spatial metric 3 – Index of overlap

This index is proposed to indicate the displacement of a resource from its traditional, pristine or desired distribution. A reference year (or distribution) is chosen and then it is compared to the other years in a time-series. As the data are aggregated onto a 0.1 degree grid it requires only to check if the same square is occupied as in the reference distribution. The index is the fraction of occupied grids in the reference distribution that are shared. Figure 10.4.3.4.2.2 shows this index for a simple data set.

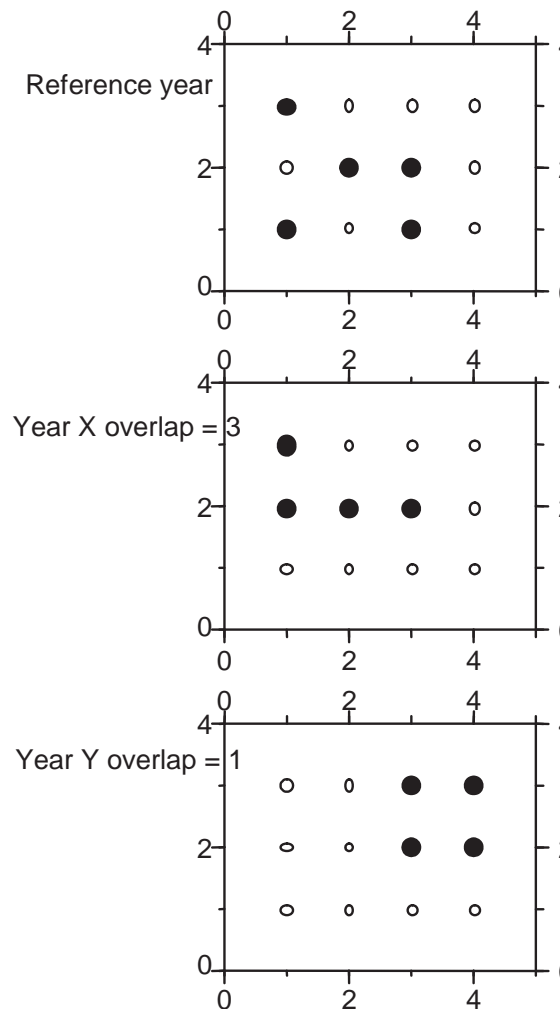


Figure 10.4.3.4.2.2 Samples of an overlay index.

10.4.3.4.3 Analysis and results

Figure 10.4.3.4.3.1 shows the abundance for the gadid group from the survey data as well as the abundance-weighted L_{max} . Abundance fell after 1982 while the weighted L_{max} showed little dynamics except for a small blip in 1992. The following figure (Figure 10.4.3.4.3.2) shows the abundance trends for animals with L_{max} above and below 100 cm. This shows that the larger animals were much more impacted over the data period but that the weighted L_{max} failed to pick up this event, probably because the larger group was such a small proportion of the total. (For plotting and to ease comparison, all indices in the following have been normalised to their mean.)

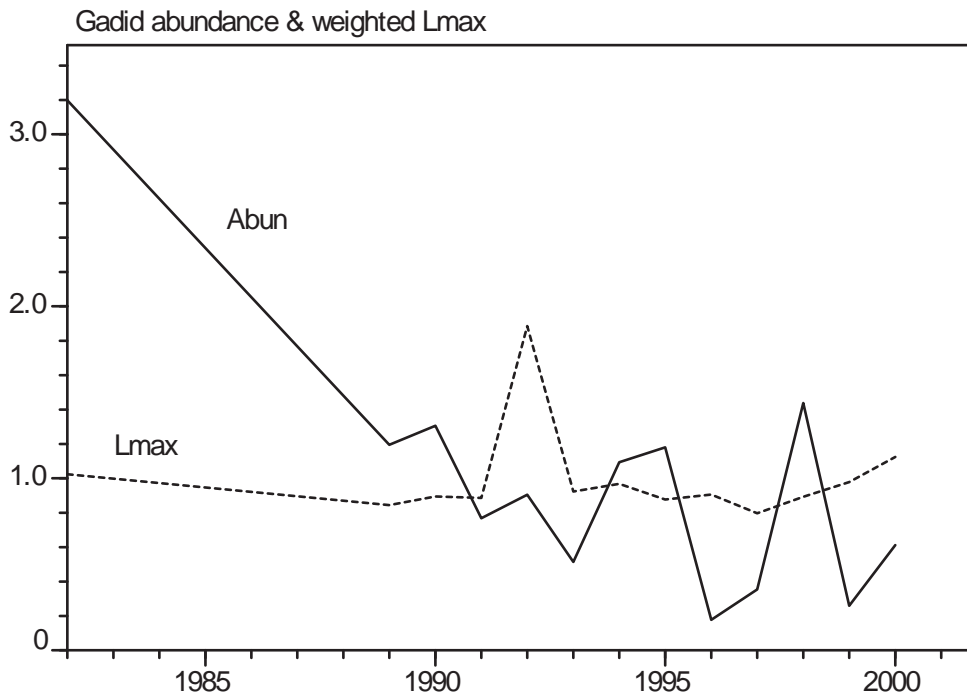


Figure 10.4.3.4.3.1 Gadid abundance L_{max} weighted by abundance.

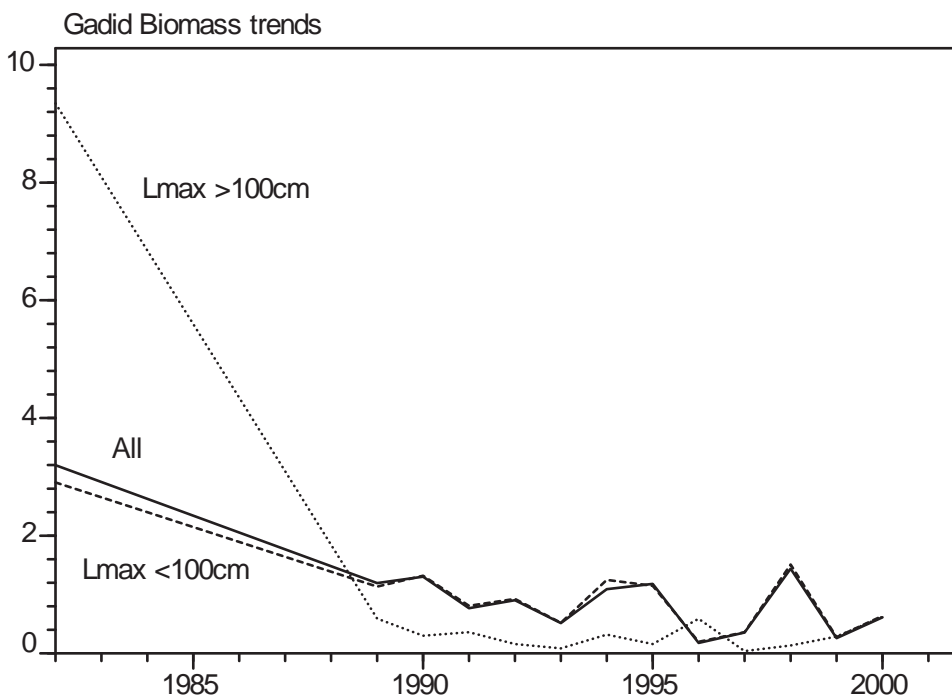


Figure 10.4.3.4.3.2 Gadid abundance after separating animals to those with L_{max} over and under 100 cm.

An analogous pair of plots are given for elasmobranchs (Figures 10.4.3.4.3.3 and 10.4.3.4.3.4). For this group of fish, there was a rise between 1982 and the next observation in 1989 in abundance which affected the weighted L_{max} . There was a spike in recruitment also in 1996 which did not affect the group's L_{max} , presumably because it was caused by animals near the mean L_{max} . The separation into size groups shows that the first event was due to large elasmobranchs, while the second was dominated by smaller fish.

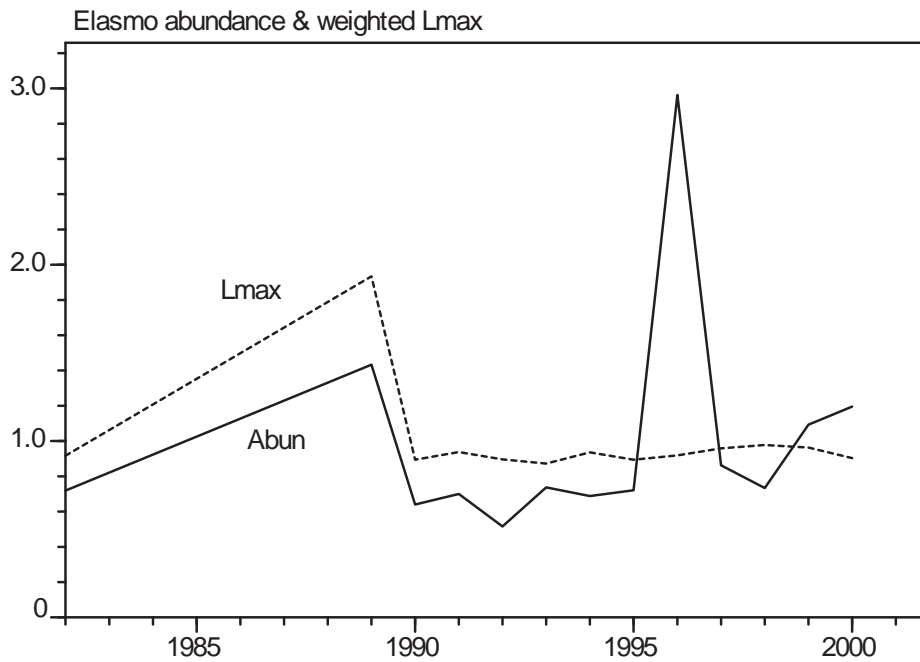


Figure 10.4.3.4.3.3 Elasmobranch abundance with and without L_{max} weighting.

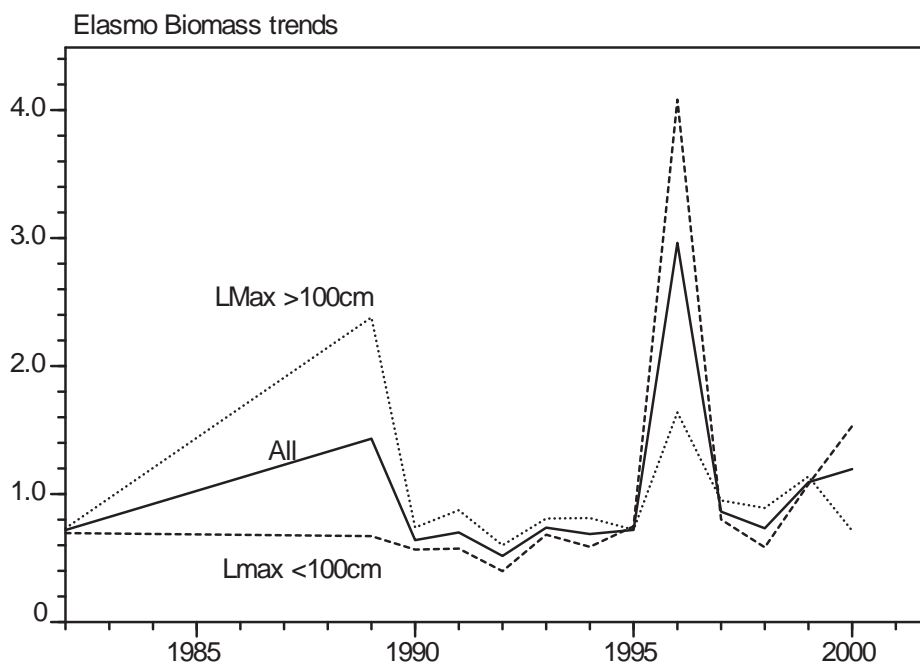


Figure 10.4.3.4.3.4 Gadid abundance after separating animals to those with L_{max} over and under 100 cm.

Figure 10.4.3.4.3.5 shows the abundance and the anomaly of the centre of biomass for the gadid group of fishes. It is difficult to infer the performance of the anomaly with this short data series although it appears to be somewhat opposite in phase to the abundance after 1989, suggested by the data from 1993, 1997, and 1998. Figure 10.4.3.4.3.6 shows a more dynamic anomaly. In 1992 there is little change in the biomass but the centre of mass moves dramatically, whereas in 1996 abundance shows a large change while the distribution metric changes very little. Further investigation is required to see if these reflect “real” events.

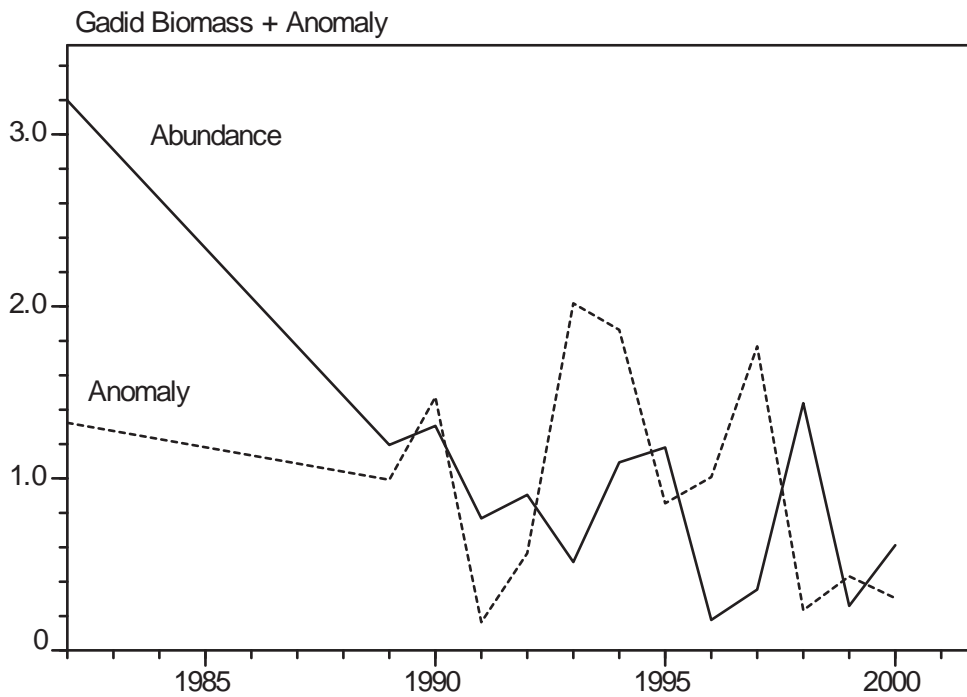


Figure 10.4.3.4.3.5 Gadid abundance and anomaly of the centre of mass.

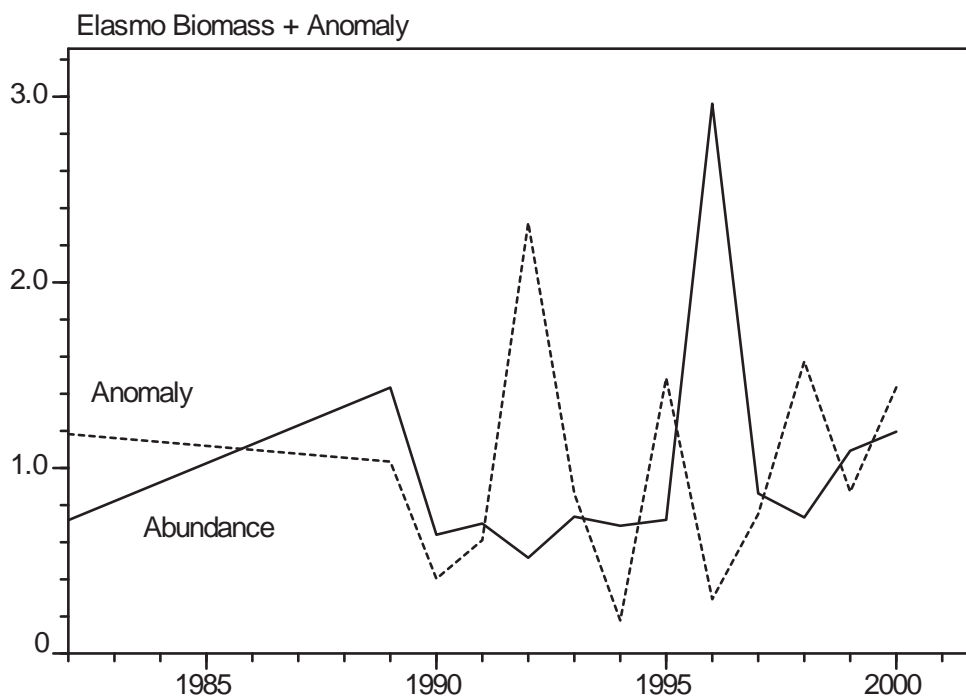


Figure 10.4.3.4.3.6 Elasmobranch abundance and anomaly of the centre of mass.

Figure 10.4.3.4.3.7 shows the abundance, contagion index, and overlap index for the gadid blue whiting (*Micromesistius poutassou*). The two spatial indices are highly correlated to the abundance. Figure 10.4.3.4.3.8 shows the abundance, contagion index, and overlap index for the elasmobranch *Scyliorhinus canicula*. These species were chosen because they were commonly seen in the survey. While the abundance has a spike in 1996, the spatial indices do not respond to the change, suggesting that the biomass distribution was not affected. Unlike the other two trends, the overlap fell after the reference year (1982), suggesting a displacement of the resource from that period.

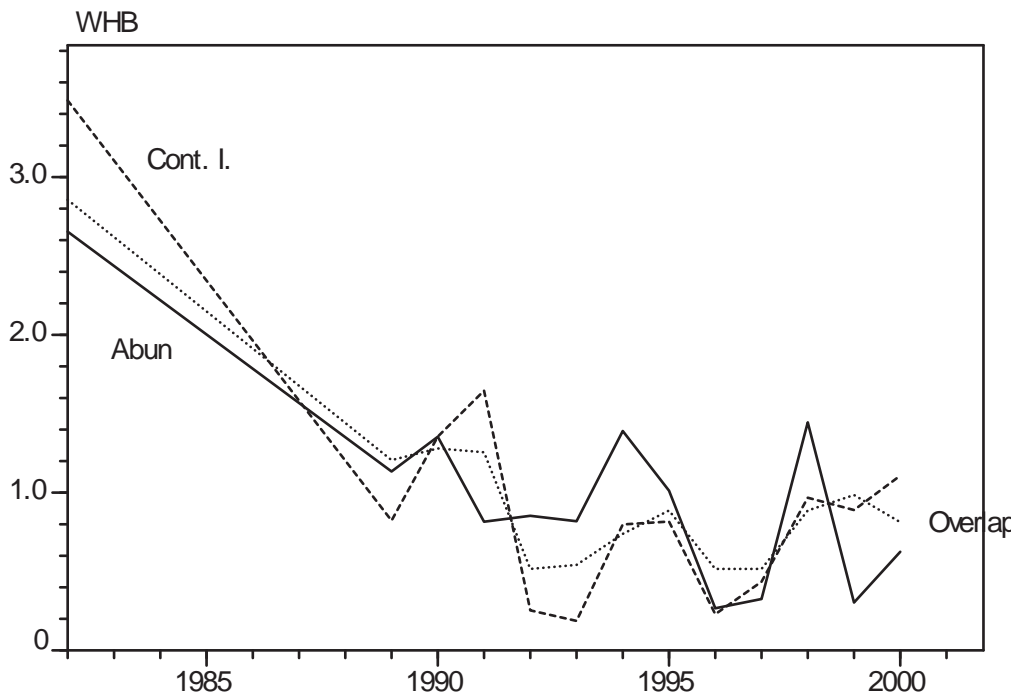


Figure 10.4.3.4.3.7 Abundance, contagion index, and overlap index for blue whiting.

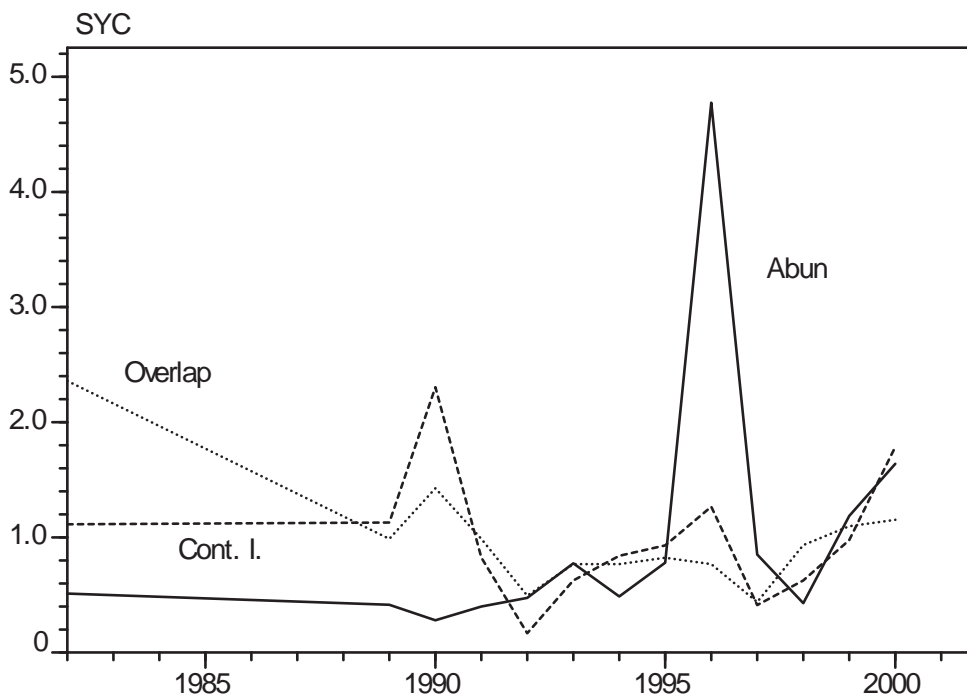


Figure 10.4.3.4.3.8 Abundance, contagion index, and overlap index for the elasmobranch species *Scyliorhinus canicula*.

The gadid group trends for abundance, contagion, and overlap are shown in Figure 10.4.3.4.3.9 and the three trends are quite similar. The indices for the elasmobranch group show more divergence (Figure 10.4.3.4.3.10). The overlap index fell even more than was seen in the single elasmobranch species shown. The contagion increases with the increase in abundance in 1996, suggesting that for a number of elasmobranch species, the increase was localised.

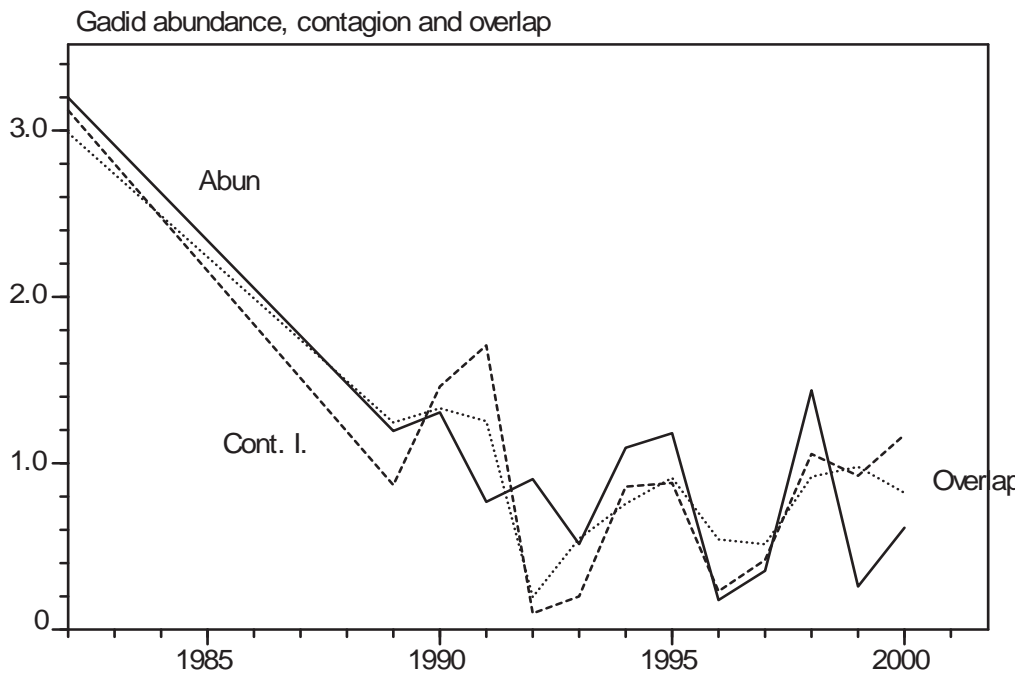


Figure 10.4.3.4.3.9 Abundance, contagion index, and overlap index for the gadid group of species.

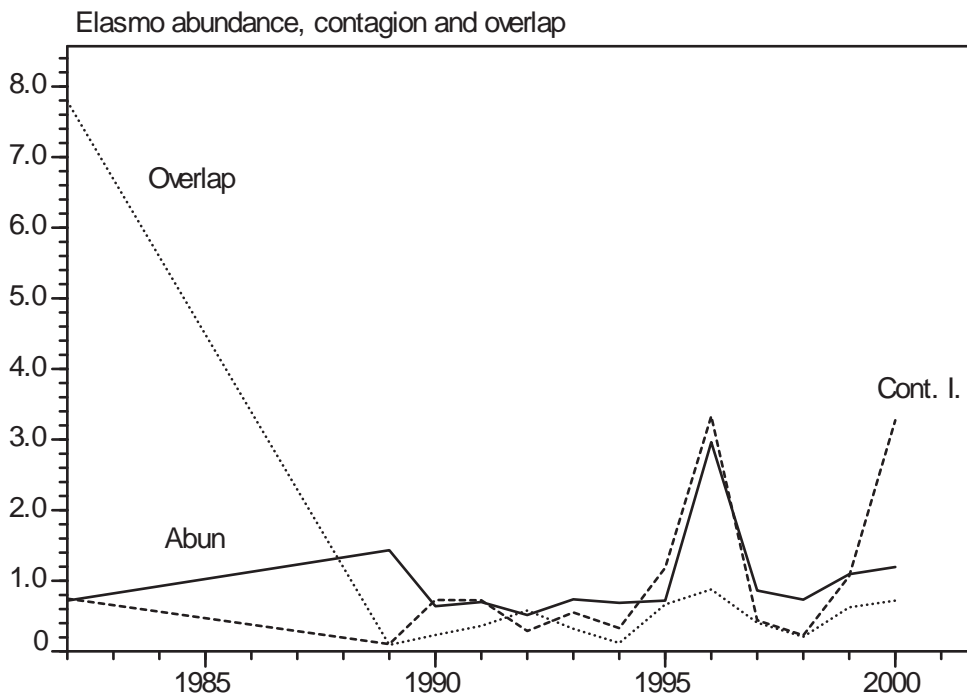


Figure 10.4.3.4.3.10 Abundance, contagion index, and overlap index for the elasmobranch group of species.

Thus, these results should be considered only as illustrations of the metrics. Even if all the analytical tools are working properly, the data are not sufficient to select among the proposed indices; none failed conspicuously, nor did any excel. Further research should be conducted in three areas: expansion to other sets of data; refinement of the metrics; and the development of a more methodical screening procedure.

10.5 Concluding thoughts and way forward

Work remains to carry many of these analyses further. Although every effort was made to assure error-free analyses, the Working Group set-up did not allow thorough review of all analyses by all WGECO members. Furthermore, not all the hypotheses proposed could be tested, without reformatting or revisions to the data that were not possible for the Working Group. Hence, conclusions in these sections are preliminary, although it is important to highlight that many results are consistent with the predictions made about changes in life history characteristics. Nevertheless, at this stage the analyses were not detailed enough to be used by themselves to justify strong conclusions about the sensitivity and information content of life history traits relative to fishing effort. In particular, a better understanding is needed of how

cases where predictions from life history theory were supported differed from the cases where either the predicted patterns were not found or where significant patterns actually were the opposite of the predictions from theory. WGECCO feels that such analyses are important, because, along with impacts on physical habitat features, the effects of fishing on life history properties of species are some of the most lasting effects of fishing (ICES, 2000), and the work should be continued within ICES.

References

- Branton, R., and Black, J. 2000. 2000 summer groundfish survey update for selected Scotia-Fundy groundfish stocks. DFO Canadian Stock Assess. Res. Doc. 2000/129. 61 pp.
- Cardador, F., Sánchez, F., Pereiro, F.J., Borges, M.F., Caramelo, A.M., Azevedo, M., Silva, A., Pérez, N., Martins, M.M., Olaso, I., Pestana, G., Trujillo, V., and Fernandez, A. 1997. Groundfish surveys in the Atlantic Iberian waters (ICES Divisions VIIIc and IXa): history and perspectives. ICES CM 1997/Y: 08.
- Dann, N. 2001. A spatial and temporal diversity index taking into account species rarity, with an application to the North Sea fish community. ICES CM 2001/T:04.
- Gomes, M.C., Serrão, E., and Borges, M.F. 2001. Spatial patterns of groundfish assemblages on the continental shelf of Portugal. *ICES Journal of Marine Science*, 58(3):633–647.
- Greenstreet, S.P.R., and Hall, S.J. 1996. Fishing and the ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. *Journal of Animal Ecology*, 65: 577–598.
- Greenstreet, S.P.R., and Rogers, S.I. 1999. The effects of fishing on non-target fish species. *In* Effects of fishing on non-target species and habitats: biological conservation and socio-economic issues. Ed. by M.J. Kaiser and S.J. de Groot. Blackwell Science, Oxford. 416 pp.
- Greenstreet, S.P.R., Spence, F.E., and McMillan, J.A. 1999a. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in structure of the North Sea groundfish assemblage between 1925 and 1996. *Fisheries Research*, 40: 153–183.
- Greenstreet, S.P.R., Spence, F.E., Shanks, A.M., and McMillan, J.A. 1999b. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. II. Trends in fishing effort in the North Sea by U.K. registered vessels landing in Scotland. *Fisheries Research*, 40: 107–124.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54: 427–432.
- Huston, A.H. 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press. 681 pp.
- ICES. 1999. Report of the International Bottom Trawl Survey Working Group. ICES CM 1999/D:2.
- ICES. 2000. Report of the Working Group on Ecosystem Effects of Fishing Activities. ICES CM 2000/ACME:02.
- Jennings, S., Reynolds, J.D., and Mills, S.C. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London*, 265: 1–7.
- Jennings, S., Greenstreet, S.P.R., and Reynolds, J. 1999a. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, 68: 617–627.
- Jennings, S., Alvsvag, J., Cotter, A.J., Ehrich, S., Greenstreet, S.P.R., Jarre-Teichmann, A., Mergardt, N., Rijnsdorp, A.D., and Smedstad, O. 1999b. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. III. International fishing effort in the North Sea: an analysis of spatial and temporal trends. *Fisheries Research*, 40: 125–134.
- Jennings, S., Warr, K.J., Greenstreet, S.P.R., and Cotter, A.J.R. 2000. Spatial and temporal patterns in North Sea fishing effort. *In* Effects of Fishing on Non-Target Species and Habitats: Biological, Conservation and Socio-economic Issues. Ed. by M.J. Kaiser and B. de Groot. Blackwell Science, Oxford.
- Lindeboom, H.J., and de Groot, S.J. (Eds.) 1998. IMPACT II. The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystem. NIOZ-Rapport 1998-1, RIVO-DLO Report C003/98. 404 pp.
- Paloheimo, J.E., and Dickie, L.M. 1964. Abundance and fishing success. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.* 155: 152–163.
- Pauly, D., Palomares, M.L., Froese, R., Sa-a, P., Vakily, M., Preikshot, D., and Wallace S. 2001. Fishing down Canadian aquatic food webs. *Can. J. Fish. Aquat. Sci.* 58: 51–62.
- Piet, G.J. 2001. Development of ecological quality objectives for the North Sea fish community. ICES 2001 working document.
- Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., and Tortonese, E. (Eds.). 1984. *Fishes of the North-eastern Atlantic and the Mediterranean*. UNESCO, Paris. Vols I, II and III. 1473 pp.

Titles Published in the ICES Cooperative Research Report Series

No.	Title	Price (Danish Kroner)
273	Guidance on the application of the Ecosystem Approach to Management of human activities in the European marine environment	<i>In press</i>
272	Ecosystem Effects of Fishing: Impacts, Metrics and Management Strategies	<i>In press</i>
271	Vector Pathways and the Spread of Exotic Species in the Sea. 25 pp.	60
270	The <i>Nephrops</i> fisheries of the Northeast Atlantic and Mediterranean – A review and assessment of fishing gear design. 38 pp.	50
269	The Annual ICES Ocean Climate Status Summary 2003/2004. 32 pp.	60
268	The DEPM Estimation of Spawning-stock Biomass for Sardine and Anchovy. 87 pp.	90
267	Report of the Thirteenth ICES Dialogue Meeting: Advancing scientific advice for an ecosystem approach to management: collaboration amongst managers, scientists, and other stakeholders. 59 pp.	50
266	Mesh Size Measurement Revisited. 56 pp.	80
265	Trends in important diseases affecting the culture of fish and molluscs in the ICES area 1998–2002. 26 pp.	40
264	Alien Species Alert: <i>Rapana venosa</i> (veined whelk). 14 pp.	50
263	Report of the ICES Advisory Committee on the Marine Environment, 2003. 227 pp.	150
262	Report of the ICES Advisory Committee on Ecosystems, 2003. 229 pp.	170
261	Report of the ICES Advisory Committee on Fishery Management, 2004 (Parts 1–3). 975 pp.	430
260	Stockholm 1999 Centenary Lectures. 48 pp.	170
259	The 2002/2003 ICES Annual Ocean Climate Status Summary. 29 pp.	150
258	Seabirds as Monitors of the Marine Environment. 73 pp.	200
257	Proceedings of the Baltic Marine Science Conference. 334 pp.	420
256	Report of the ICES Advisory Committee on the Marine Environment, 2002. 155 pp.	270
255	Report of the ICES Advisory Committee on Fishery Management, 2002. (Parts 1–3). 948 pp.	1200
254	Report of the ICES Advisory Committee on Ecosystems, 2002. 129 pp.	250
253	ICES Science 1979–1999: The View from a Younger Generation. 39 pp.	170
252	Report of the ICES/GLOBEC Workshop on the Dynamics of Growth in Cod. 97 pp. (including CD-Rom from ICES ASC 2001)	220
251	The Annual ICES Ocean Climate Status Summary 2001/2002. 27 pp.	180
250	ICES/GLOBEC Sea-going Workshop for Intercalibration of Plankton Samplers. A compilation of data, metadata and visual material, 2002. 34 pp.	190
249	Report of the ICES Advisory Committee on Ecosystems, 2001. 75 pp.	200
248	Report of the ICES Advisory Committee on the Marine Environment, 2001. 203 pp.	310
247	Effects of Extraction of Marine Sediments on the Marine Ecosystem. 80 pp.	200
246	Report of the ICES Advisory Committee on Fishery Management, 2001. (Parts 1–3). 895 pp.	1170
245	The Annual ICES Ocean Climate Status Summary 2000/2001. 21 pp.	150
244	Workshop on Gadoid Stocks in the North Sea during the 1960s and 1970s. The Fourth ICES/GLOBEC Backward-Facing Workshop. 55 pp.	160
243	Report of the 12 th ICES Dialogue Meeting (First Environmental Dialogue Meeting). 28 pp.	130
242	Report of the ICES Advisory Committee on Fishery Management, 2000. (Parts 1–3). 940 pp.	1100

No.	Title	Price (Danish Kroner)
241	Report of the ICES Advisory Committee on the Marine Environment, 2000. 263 pp.	370
240	Report of the Young Scientists Conference on Marine Ecosystem Perspectives. 73 pp.	170
239	Report of the ICES Advisory Committee on the Marine Environment, 1999. 277 pp.	350
238	Report on Echo Trace Classification. 107 pp.	200
237	Seventh Intercomparison Exercise on Trace Metals in Sea Water. 95 pp.	190
236	Report of the ICES Advisory Committee on Fishery Management, 1999. (Part 1 and Part 2). 821 pp.	920
235	Methodology for Target Strength Measurements (With special reference to <i>in situ</i> techniques for fish and mikronekton). 59 pp.	160
234	Report of the Workshop on Ocean Climate of the NW Atlantic during the 1960s and 1970s and Consequences for Gadoid Populations. 81 pp.	180
233	Report of the ICES Advisory Committee on the Marine Environment, 1998. 375 pp.	440
232	Diets of Seabirds and Consequences of Changes in Food Supply. 66 pp.	170
231	Status of Introductions of Non-Indigenous Marine Species to North Atlantic Waters 1981–1991. 91 pp.	190
230	Working Group on Methods of Fish Stock Assessment. Reports of Meetings in 1993 and 1995. 259 pp.	330
229	Report of the ICES Advisory Committee on Fishery Management, 1998. (Part 1 and Part 2). 776 pp.	900
228	Report of the 11 th ICES Dialogue Meeting on the Relationship Between Scientific Advice and Fisheries Management. 37 pp.	140
227	Tenth ICES Dialogue Meeting (Fisheries and Environment in the Bay of Biscay and Iberian Region: Can the Living Resources Be Better Utilized). 30 pp.	130
226	Report on the Results of the ICES/IOC/OSPARCOM Intercomparison Programme on the Determination of Chlorobiphenyl Congeners in Marine Media – Steps 3a, 3b, 4 and Assessment. 159 pp.	250
225	North Atlantic – Norwegian Sea Exchanges: The ICES NANSEN Project. 246 pp.	320
224	Ballast Water: Ecological and Fisheries Implications. 146 pp.	230
223	Report of the ICES Advisory Committee on Fishery Management, 1997. (Part 1 and Part 2). 780 pp.	760
222	Report of the ICES Advisory Committee on the Marine Environment, 1997. 210 pp.	250
221	Report of the ICES Advisory Committee on Fishery Management, 1996. (Part 1 and Part 2). 642 pp.	660
220	Guide to the Identification of North Sea Fish Using Premaxillae and Vertebrae. 231 pp (including 300 photographs)	560
219	Database Report of the Stomach Sampling Project, 1991. 422 pp.	410

These publications may be ordered from: ICES Secretariat, H. C. Andersens Boulevard 44–46, DK-1553 Copenhagen V, Denmark, fax: +45 33 93 42 15, e-mail: info@ices.dk. An invoice including the cost of postage and handling will be sent. Publications are usually dispatched within one week of receipt of payment. Further information about ICES publications, including ordering and payment by credit card, cheques and bank transfer, may be found at: www.ices.dk/pubs.htm.