H:\brm\multi\carr_cap1_09102001.doc/ps
Oct. 9, 2001

# Spawner-Recruit Relationships and Fish Stock Carrying Capacity in Aquatic Ecosystems

Brian R. MacKenzie[1], Ransom A. Myers[2] and Keith G. Bowen[3]

(1) Danish Institute for Fisheries Research, Department of Marine Ecology and Aquaculture, Kavalergården 6, DK-2920 Charlottenlund, Denmark
(2) Killam Chair of Ocean Studies, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1
(3) Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

Keywords: recruitment variability, stock-recruitment, fisheries, carrying capacity, ecosystems, production, habitat

To be submitted to Mar. Ecol. Prog. Ser. or Can. J. Fish. Aquat. Sci.

MacKenzie, Myers, Bowen. Spawner-recruit relationships and fish stock carrying capacity in aquatic ecosystems. To be submitted to Mar. Ecol. Prog. Ser. or Can. J. Fish. Aquat. Sci.

Abstract:

Few marine ecologists have addressed important questions of the relative productivity and carrying capacity of different ecosystems to support fish populations. Whereas many researchers have investigated interannual variability in recruitment within a stock, we ask if relationships between spawner abundance and subsequent recruitment are similar among populations (N = 3-20) of the same species, and among species (N = 14). We find that a large and significant amount of the variation ($R^2$ = 75-95%) in mean log recruitment is explained by mean log spawner biomass when the spawner-recruit relationship is examined among populations of the same species. The slopes of these relationships are close to 1 (i. e., proportional). However mean recruitment per spawner varies greatly among species (range 3-10) and mean recruit production per spawner is more variable among populations of some species (cod, *Gadus morhua*) than others (sole, *Solea solea*). Some ecosystems allowed cod, haddock (*Melanogrammus aeglefinus*) and herring (*Clupea harengus*) populations to produce an average of ca. 8-fold more recruits per spawner than other ecosystems. Also, the abundance of at least one species (cod) is strongly related to habitat size. Reasons for the differences in recruit production per spawner between ecosystems are unclear, but the differences themselves may need to be considered in marine ecosystem management contexts.

Keywords: recruitment variability, stock-recruitment, fisheries, carrying capacity, ecosystems, production, habitat

## Introduction:

Recent meta-analytical and comparative studies of fish population dynamics have shown that different fish stocks and species have common patterns in their life history and population dynamics. For example, maximum lifetime reproductive rate in marine fish populations is relatively constant both within and between 100's of populations (Myers et al. 1999), and some closely related species occupying similar ecosystems respond to key environmental signals in similar fashion (Bakun 1996). These results became evident only after data and information from several stocks and species were combined and standardized in ways that enabled fair and unbiased comparisons.

One of the most important relationships in fisheries ecology is that between egg production (e.g. spawning stock biomass) and recruitment. This relationship is typically uncertain because of errors in measurement of both recruitment and egg production (Hilborn & Walters 1992, Marshall et al. 1998) and because of environmental processes whose impact on young fish survival varies between years (Watanabe et al. 1995, Bakun 1996, Jarre-Teichmann et al. 2000). The relative importance of these sources of uncertainty is unknown. Nevertheless, experience has shown that when fish stocks are reduced to sufficiently low levels, they produce fewer recruits (Myers & Barrowman 1996).

In this report we consider three scales of recruitment variability and evaluate whether variability at any of these scales is functionally related to spawner biomass. The scales of variability we consider are: 1) interannual variability within a stock; 2) variability among stock within a species; and 3) variability among species. We chose to investigate recruitment variability at these scales because studies of the relative importance of spawner biomass and other factors that might affect recruitment, particularly at the among-stock and among-species levels, have received very little attention among fisheries biologists and oceanographers. As a result, some major comparative questions in marine ecology and fisheries population dynamics remain unclear. For example, do some areas of the sea (e. g., Scotian Shelf) produce more new fish (e.g., haddock) than other regions (e.g., North Sea) after allowing for differences in spawner biomass, and is the mean recruitment per spawner biomass similar for different species throughout their ranges?

We therefore investigate spawner-recruit relationships at multiples scales and the relative roles of spawner biomass and other variables on recruitment at these scales. We hypothesize that at larger scales (e. g., among stocks) the relative influence of spawner biomass on recruitment will increase and that recruitment per spawner will be relatively similar among stocks and species. Alternatively, differences among stocks would suggest that some regions are more productive than others, or have a higher carrying capacity, in terms of the production of new recruits per unit spawning biomass. These issues will be evaluated using the extensive data compilation of Myers et al. (1995; www.mscs.dal.ca/~myers/welcome.html).

## Methods:

Data sources:

Estimates of spawner and recruit abundance were extracted from a comprehensive database containing over 800 time series of fisheries data from all over the world (Myers et al. 1995). Our analyses were confined to species with multiple stocks, and those which were among the most commerically important. We used stocks with at least 10 pairs of spawner recruit data that could be standardized to the same units. If a species had at least 4 stocks it was included. We also used all hakes (members of the genus *Merlucius*) and 3 tuna species for comparison. The species, stocks and spawner-recruit data used are available at http://www.mscs.dal.ca/~myers/papers /AmongStockSR.dat.

The spawner abundance for year t for cohort j, $S_{tj}$, is given in numbers of spawners (a proxy for egg production) for Pacific salmon species and biomass of spawners for other species. For salmon species, recruits, $R_{tj}$, is simply the number of returning spawners from that cohort before fishing occurs. For other species recruitment occurs before the age of spawning and differs within and between stocks (0 - 5 years). Since numbers-at-age decline over time, recruitment estimates from stocks with different recruit ages must be converted to standard units. The recruitment data within each stock were standardized by converting the raw numbers-at-age to the production of new spawners during its expected lifetime in the absence of fishing. Using this convertion, the units of recruitment are the same as the units of spawners; this allows easy comparisons among populations and species.

We will denote stocks by subscript j. The standardized recruitment is calculated as the product of the raw recruitment, i.e. $N_{a_r, tj}$, in numbers at age $a_r$, and is multipliplied by the spawner biomass produced per recruit in the absence of fishing, $SPR_{F=0}$ . The value for a cohort born in year t, is given by:

$$R_{tj} = SPR_{jF=0} \cdot N_{a_r, tj}$$

where

$$SPR_{jF=0} = \sum_{a=a_r}^{A_j} w_{ja} p_{ja} e^{-\sum_{c=1}^{a-1} M_{jc}}$$

??? this did not come through in my copy????????????????

(Myers et al. 1996) where

$N_{ja}$ = numbers at age for cohort, $w_{ja}$ = weight at age a, $p_{ja}$ = proportion of fish mature at age a, $A_j$ = maximum age, $a_r$ = age at recruitment, and $M_{jc}$ = natural mortality at age c.

Statistical analyses:

Statistical analyses consisted of scatterplots and regression analyses (dependent and independent variables were recruitment and spawner abundance). We first considered recruitment variability among stocks within a species, both for annual data and for stock averages. A second set of analyses considered recruitment variability among species and used stock-specific mean spawner-recruit data. For both sets of analyses, the spawner-recruit data were $\log_{10}$ transformed (Hennemuth et al. 1980). Residual variation from the among-stocks log spawner - log recruitment relationship was estimated and ranked according to the different stocks.

In order to compare recruitment variation among species, we needed the mean log recruitment and mean log spawner biomass for a given stock of a species. This was calculated as folllows:

$$\log R_j = \frac{\sum_t \log R_{tj}}{n_j},$$

$$\log S_j = \frac{\sum_t \log S_{tj}}{n_j},$$

where $n_j$ is the number of paired spawner recruit observations.

A linear regression analysis of the variability in $\log R_j$ explained by $\log S_j$ yields relationships for a species of the form:

$$\log R_j = \gamma \log S_j + \log \beta.$$

If $\gamma$ is constrained to be equal to 1 (see results and Fig. 3b), then $\log \beta$ is the mean of $\log R_j - \log S_j$.

Habitat area estimates:

We investigated how habitat size affects recruit and spawner abundance in one species, cod *Gadus morhua.* Estimates of habitat area (area of sea bottom in each region between 0 and 300 m) were obtained from Myers et al. (2001) and were used in exploratory scatterplots and regression analyses.

## Results:

*Variability within a stock:*

We first examine the variability in recruitment among years and stocks for 4 species (Fig. 1). As is typical for many species, the within-stock (interannual) variability in recruitment is weakly related to spawning biomass. This is best demonstrated with plaice (*Pleuronectes platessa*) data (Fig. 1d): several stocks show wide variability in recruitment for a relatively small range in spawner biomass. Interannual recruitment variability is also higher for some species than others. For example, in some years, recruitment in some years for some haddock and herring stocks was below the 1:1 stock replacement line (Fig. 1b, c), whereas most of the points for cod and plaice lie above the line (Fig.1a, d). See Myers (2001) for a review of within population variability in recruitment.

*Variability among stocks within a species:*

The second level of recruitment variability we consider is among stocks within a species. Strong relationships between recruitment and spawner biomass are evident. This pattern is obvious when comparing either interannual spawner-recruitment data (Fig. 1) or stock-specific averages (Fig. 2). In the latter case, mean log spawner biomass nearly always explains > 70% ($P < 0.05$) of the variation ($R^2$) in mean log recruitment (Fig. 3a). Less of the variation was explained by spawner abundance for gadoid species (lower $R^2$) than the salmonid and flatfish species (Fig. 3a). The slope of the relationships between mean log recruitment and mean log spawner biomass across stocks were approximately unity for nearly all species (slope ca. 1 on log-log scale); only plaice and sockeye salmon had slopes which nominally differed significantly from 1 (Fig. 3b).

Some geographic regions seem to produce more recruits per unit spawner biomass than others (Fig. 4: residual analysis plots). When the residuals from the mean log recruitment-mean log spawner biomass relationships are back-transformed to arithmetic units, the range in residual recruitment relative to the mean is ca. ± 3-fold among regions, or ca. 8-fold when comparing sites with the lowest and highest residual variation.

*Variability among species:*

The third level of recruitment variation is that among species. Some species produced more recruits per spawner biomass than others (Fig. 5). That is, mean log recruit-mean log spawner regression relationships for some species were higher above the 1:1 replacement line than others (Fig. 5). If the slope of this relationship is assumed equal to 1 (Fig. 3b), then the mean log recruit per log spawner biomass (log $\beta$) for each of 14 species can be estimated (see methods).

The estimate of $\beta$ ranged from 3-10, and salmonid species generally had low $\beta$'s while cod and plaice had higher values (Fig. 6a). There were large differences in the variability (standard deviation) of $\beta$ among species (Fig. 6b). The variability in mean log recruitment per mean log spawner biomass among cod stocks (and the other Gadoids) is greater than that for herring and salmonids.

*Abundance-area relationships:*

The high correlation between log recruitment and log spawner biomass among stocks within a species is at least partly due to combining stocks inhabiting regions of different sizes. For one species (cod), habitat area has a significant influence on both recruit and spawner abundance (Fig. 7; Table 2). Mean log recruitment was highly correlated to both mean log spawner biomass and log area, and log spawner biomass and log area were themselves correlated. Log area did not explain additional significant variation in mean log recruitment when included in a multiple regression analysis with mean log spawner biomass (Table 2).

## Discussion:

### General:

This paper raises issues which have been largely overlooked by fisheries population biologists. We have found that recruitment variability within species is clearly related to spawner biomass and the nature of this relationship (e. g., its functional form, residual variability) is relatively similar among species. We have also observed that recruitment per spawner among stocks is variable throughout a species' range. This result suggests that carrying capacity for new recruit production differs between ecosystems.

### Spawner-recruit relationships:

In this section we consider three levels of recruitment variability: interannual variability within a stock, among stock variability within a species and among species variability.

#### i) interannual variability within a stock:

For most stocks the spawner-recruitment relationship is typically dominated by large unexplained variability (Cushing 1995, Myers & Barrowman 1996). This pattern was also evident in our analyses. Much research effort is attempting to clarify and distinguish processes responsible for this variation (e. g. (Campbell 1997, Coombs et al. 1998) although with little success for most stocks (Myers 1998). In most cases the expected recruit production for all stocks and all years was above the 1:1 replacement line. However, stock collapses due to low recruitment per spawner biomass were evident in some cases.

As examples, the Norwegian spring-spawning herring and some haddock stocks have had several years of extremely low recruitment for the given spawning stock size. This pattern indicates that under some circumstances spawner biomass itself will not be sufficient for strong yearclasses because other factors (e. g., environmental effects on pre-recruit survival) negatively affect recruitment. If several years of poor environmental conditions occur in a relatively short period, particularly when combined with high fishing mortality, stock levels will quickly decrease (Watanabe et al. 1995, Wada & Jacobson 1998, Jarre-Teichmann et al. 2000). Conversely, average or high recruitment per unit spawning stock may not be sufficient to prevent stock collapses when fishing mortality of juveniles and pre-recruits is high. For example, when cod stocks in the northwest Atlantic collapsed in the late 1980's-early 1990's, recruitment was apparently sufficient to replace spawning stock levels existing at that time (Myers et al. 1996, Myers et al. 1997).

ii) recruitment variability among stocks within a species

Variability in recruitment at scales other than within-stock (i. e. interannual) has received much less attention by fisheries biologists and oceanographers.

We have shown that relationships between log spawner abundance and log recruitment among stocks are highly significant and robust. The highly significant effect of log spawner abundance on log recruitment at the large space-time scales (i.e., among stocks, and for time periods of 2-3 decades) considered in this study overrides much of the potential regional or ecosystem effect on recruitment. Differences in recruit production per spawner (i.e. the residual variation from the species-specific regression models), although ca. 8 fold, are *comparatively* small in most of the among-stock spawner–recruit relationships. Log recruitment in stocks throughout a species range was close to the overall mean log recruitment (for a given log spawner biomass) as represented by the spawner-recruit regression relationship, despite large differences in environmental and biological conditions (e. g., temperatures, predation, etc.) that exist between ecosystems.

The strong relationships between log spawning stock size and log recruitment among stocks indicates that spawner biomass dominates other factors (including regional environmental influences and various measurement errors) that determine long-term mean recruitment levels. This result is similar to some previous species-level spawner-recruitment analyses (Garrod & Knights 1979, Myers & Barrowman 1996, Jakobsen 1996). The strength of the among-stocks spawner-recruit relationships is partly a consequence of abundance-area relationships. At the large spatial scales of entire stocks, differences in spawner biomass associated with regions of different size clearly have a much stronger impact on recruitment than other variables. Although most of our log spawner-log recruit relationships explained high amounts of recruitment variation, the relationships for some species (e. g., cod, haddock) were more variable than relationships for other species (flatfishes). The variation within the cod and haddock relationships suggests that some ecosystems occupied by these species may be more productive in terms of recruit production per spawner biomass unit than others (see below: *Carrying capacity of different ecosystems and among-stocks recruitment variability*).

iii) recruitment variability among species

Spawner-recruit relationships at the species level are *approximately* similar in terms of slope (ca. 1) and explained variation. This pattern is robust despite differences in life-history and habitat (marine, anadromous, freshwater). Differences in spawner-recruit slopes among species were relatively small, and some species (e. g., cod, herring) were more variable than others (plaice, sole, salmonids). Our finding that recruitment per spawner biomass is more variable within gadoid species and herring than within flatfish species is consistent with an earlier comparison of recruitment among species (Leggett & Frank 1997).

In general, all species and stocks produced on average an excess of recruits to replace the spawners in the population. However, there were some important differences in recruit production per spawner among species (range 3-10). In particular, cod appears to be one of the most productive species while salmonids appear to be the least productive species, although reasons for these differences are not clear and may be related to interactions between exploitation and density-dependent mortality. The high recruit-per-spawner potential of cod, especially when compared with other species, might partly explain why many cod stocks resisted collapse for many years despite high exploitation rates (Myers et al. 1996, Myers et al. 1997). These differences need further investigation.

Carrying capacity of different ecosystems and among-stocks recruitment variability:

Differences in recruit production per unit spawner abundance exist among stocks and therefore between ecosystems occupied by these stocks. In the case of cod, haddock and herring, some regions on average have produced ca. 8-fold more recruits than other regions over the last 3 decades. We have shown using alternative, more rigorous methods (stock-specific Beverton-Holt spawner-recruit curves fitted to the same cod data using Bayesian methods and area-standardized data), that differences in carrying capacity for cod exist, and are large (ca. 10-fold; (Myers et al. 2001). Both of our studies suggest that ecosystems differ in their ability to produce new recruits of a given species *even after allowing for differences in spawner biomass*. In comparison, the regional variability in maximum reproductive rate of cod at low abundance is essentially constant among stocks (30-35 new spawners per fish; (Myers et al. 1999)). We interpret the differences in recruit production per spawner among stocks as differences in carrying capacity for recruit production and survival.

The ecological processes that generate differences in carrying capacity are not clear, particularly after the influence of spawner biomass is accommodated in the analysis. However the processes might include differences in primary production rates, interactions with other species (e. g., competition, predation: (Myers et al. 2001, Swain & Sinclair 2000)) and abiotic factors (e. g., temperature: (Planque & Fredou 1999, Brander 2000). In one species (cod), we demonstrated that smaller regions produced as many recruits per spawner as larger regions.

The results of our analyses apply to fishing/environmental conditions typical for the last 2-4 decades. This is the time period covered by most of the spawner–recruit data in our analyses. Carrying capacities and stock dynamics under different time periods could be different because of changes in food webs (e. g., predators, competitors) and environmental variability. For example, model simulations show that carrying capacities for consumers in ecosystems *having the same primary productivity* can be increased as much as 6 fold, depending on food web structure (Christensen & Pauly 1998), and environmental changes associated with carrying capacity are believed responsible for a 75-fold increase in recruitment per spawner biomass of Japanese sardine between 1951-70 and 1971-95 (Wada & Jacobson 1998).

The dynamics of carrying capacity and stock productivity may be relevant for fisheries management. Stock rebuilding efforts following stock collapses could require far more (less) time, if conditions have switched to a lower-(higher) capacity regime once the stock has been reduced, given that maximum reproductive rates within populations of a fish species are relatively constant (Myers et al. 1999). Such a switch in carrying capacity may have occurred both in Atlantic Canada where recovery of cod stocks is taking longer than expected from single-species models of stock biology (Sinclair et al. 1997, Hutchings 2000) and in the north Pacific where climate-related regime shifts influence fish production (Beamish papers). Detecting such changes requires long time series which are becoming increasingly available.

## Habitat area relationships:

We have observed that cod abundance (both spawner biomass and recruits) increases logarithmically with a simple definition of habitat size. The slope (0.8 ± 0.2) of this relationship suggests that as a first approximation, and based on the time series used to construct these relationships, each additional km$^2$ of habitat area might provide on average ~1 additional kg of cod spawner and recruit biomass.

The abundance-area patterns suggest that space (or factors associated with space) sets the overall limit to cod abundance within the different regions. Abundance-area relationships have also been reported for herring (Iles & Sinclair 1982; Hay & McCarter 1997) and sole (Rinjsdorp et al. 1992). For example, mean herring recruitment in the northwest Atlantic was related to area of larval nursery areas (“retention zones”; Iles & Sinclair 1982) and maximum herring biomass for 14 populations was strongly correlated with summer feeding habitat area, which was assumed to be represented by continental shelf area (0-200 m). The range of herring densities reported by Hay and McCarter (1997) is 0.2-10 t/km$^2$. In comparison we have shown elsewhere (Myers et al. In press) that the maximum cod spawner biomass density in 20 cod populations has approximately the same range (ca. 0.1 – 8 t/km$^2$) as that observed for the herring populations.

The abundance-area relationship that we identify for cod is an approximation because of our simple definition of habitat size, and also because of the strong correlation of spawner biomass with habitat size. We assumed for cod that the limiting factors for recruit production were processes correlated with area of the sea bottom between 0 and 300 m depth, although the specific mechanisms that affect mortality during different lifehistory stages (egg, larval, juvenile, adult) are poorly known for cod stocks. For some stocks, density dependent processes after settlement seem most important for recruitment (Myers and Cadigan 1993; Heath and Gallego 1998), whereas for other stocks processes in the pelagic stage can be important (Swain and Sinclair 2000; Jarre-Teichman et al. 2000). Our results suggest that even though the relative importance of benthic and pelagic processes might vary between and within stocks, they are associated with habitat size.

## Conclusions:

Comparative analyses of spawner–recruit relationships have shown that most of the variation in mean log recruitment among stocks of a given species is explained by mean log spawner biomass ($R^2$ = 75-95%). These analyses have also shown that mean log recruitment is directly proportional to mean log spawner biomass (slope of the log spawner-log recruit relationship is 1) and that the production of new fish *per unit spawner biomass* varies among stocks within a species and among species. We conclude that spawner biomass explains much more of the variability in recruitment among stocks than within stocks.

Acknowledgements:

Partial funding was provided by DIFRES and a grant from the European Union (FAIR contract CT98-4122; Scientific coordinator M. Heath, Marine Laboratory, Aberdeen).

Table 1. Stock codes corresponding to symbols in Figures 1 and 2.

| | Cod | Haddock | Herring | Plaice |
|---|---|---|---|---|
| 1 | NAFO 2J3KL | NAFO 4TVW | W. Baltic SD 22-24 | ICES VIId |
| 2 | NAFO 3NO | NAFO 4X | NAFO 4-5 | ICES VIIe |
| 3 | NAFO 3Pn4RS | NAFO 5Z | Central Coast BC | Celtic Sea |
| 4 | NAFO 3Ps | Færoe Plateau | Downs stock | Irish Sea |
| 5 | NAFO 4TVn | Iceland | Georges Bank | Kattegat |
| 6 | NAFO 4VsW | North East Arctic | Gulf of Finland | North Sea |
| 7 | NAFO 4X | North Sea | Gulf of Maine | Skagerrak |
| 8 | NAFO 5Y | Rockall | Gulf of Riga | |
| 9 | NAFO 5Z | W. Scotland | Iceland (spring spawners) | |
| a | W. Baltic SD 22-24 | | Iceland (summer spawners) | |
| b | E. Baltic SD 25-32 | | Norway (spring spawners) | |
| c | Celtic Sea | | North Sea | |
| d | Færoe Plateau | | No. Strait of Georgia | |
| e | Iceland | | NW Coast Vancouver Isl. | |
| f | Irish Sea | | Prince Rupert District | |
| g | Kattegat | | Queen Charlotte Islands | |
| h | North East Arctic | | So. Strait of Georgia | |
| i | North Sea | | SW Coast Vancouver Isl. | |
| j | Skagerrak | | | |
| k | W. Scotland | | | |

Table 2. Regression statistics for relationships between cod mean recruitment, mean spawner abundance and habitat area for 20 populations. All analyses used means of $\log_{10}$ transformed data; R = recruits (kg), S = spawner biomass (kg), A = area ($km^2$). Regression coefficients are shown with 1 standard error; $R^2_{adj}$ = correlation coefficient adjusted for the number of degrees of freedom, P = probability level, RMSE = root mean square error from regression model.

| Model | $R^2_{adj}$ | $P_{overall}$ | $P_{coeff.}$ | RMSE |
|---|---|---|---|---|
| log R = 0.80 ± 0.23*log A<br>+ 4.84 ± 1.16 | 0.36 | 0.0029 | 0.0029<br>0.0006 | 0.436 |
| log S = 0.82 ± 0.24*log A<br>+ 3.72 ±1.22 | 0.35 | 0.0034 | 0.0034<br>0.0069 | 0.457 |
| log R = 0.84 ± 0.11*log S<br>+ 2.24 ± 0.85 | 0.76 | < 0.0001 | < 0.0001<br>0.0170 | 0.268 |
| log R = 0.76 ± 0.14*log S<br>+ 0.17 ± 0.18 *log A<br>+ 2.01 ± 0.88 | 0.76 | < 0.0001 | < 0.0001<br>0.3585<br>0.0365 | 0.269 |

Figure captions:

Figure 1. The interannual variation in recruitment within stocks ($\log_{10}$ recruitment (kg) and $\log_{10}$ spawning stock biomass (kg)) where each stock is identified by a number or letter code (Table 1). Data are for 20 cod (*Gadus morhua*) stocks (a), 9 haddock (*Melanogrammus aeglefinus*) stocks (b), 18 herring (*Clupea harengus*) stocks (c) and 7 plaice (*Pleuronectes platessa*) stocks. Each symbol represents 1 cohort for each stock. Note that both recruits and spawners are given in the same units. The dotted line is the replacement line, and the distance each point is above that line gives the increase of a cohort that would occur if no fishing occurred. See text.

Figure 2. Variability among stocks within a species (mean $\log_{10}$ recruitment (kg) and mean $\log_{10}$ spawning stock biomass (kg)). Data are for 20 cod stocks (a), 9 haddock stocks (b), 18 herring stocks (c), and 7 plaice stocks (d). Symbols represent different stocks (see Table 1 for symbol definitions). Each symbol represents the mean for 1 stock and the dotted line is the 1:1 replacement line, see Fig.1 and text for further details.

Figure 3. Variability among stocks within a species explained by mean $\log_{10}$ spawner biomass (kg). (a) Proportions of variation in mean $\log_{10}$ recruitment (kg) explained ($R^2$) by mean $\log_{10}$ spawning stock biomass (kg) for species living in marine and freshwater. Numbers above bars represent number of stocks used in the analyses. All regression were significant ($P < 0.05$) except for the tunas. (b) Slopes ($\pm$ st. error) of linear regression models relating mean $\log_{10}$ recruitment (kg) to mean $\log_{10}$ spawning stock biomass (kg) for species used in panel (a).

Figure 4. Variability among stocks within a species not explained by mean $\log_{10}$ spawning stock biomass. Residual variation from regression analyses of mean $\log_{10}$ recruitment (kg) vs. mean $\log_{10}$ spawning stock biomass (kg). Data are for 20 cod (a) 9 haddock (b) and 18 herring stocks.

Figure 5a, b. The variability among species. Regression lines describing the relationship between mean $\log_{10}$ recruitment (kg) and mean $\log_{10}$ spawning stock biomass (kg) for several marine, anadromous, and freshwater species. $R^2$ and slope values are presented in Figure 6 (a, b). The dotted line is the 1:1 replacement line. See also Fig.1 and text for further details.

Figure 6. Among species variation in recruitment above replacement levels. (a) Mean difference ($\log_{10} \beta$; see text for definition) between $\log_{10}$ recruitment (kg) and $\log_{10}$ spawning stock biomass (kg) across stocks within each species. (b) Standard deviation of $\log_{10} \beta$, difference between $\log_{10}$ recruitment (kg) and $\log_{10}$ spawning stock biomass (kg) across stocks within each species.

Figure 7. Among stocks variation in mean $\log_{10}$ spawner biomass (kg) and mean $\log_{10}$ recruitment (kg) explained by habitat area for cod, *Gadus morhua*. Mean $\log_{10}$ spawner biomass (kg) (a) and $\log_{10}$ recruitment (kg) (b) vs. $\log_{10}$ habitat area for 20 stocks.

# Reference List

Bakun A (1996) Patterns in the ocean: Ocean Processes and Marine Population Dynamics. Cal.Sea Grant System, NOAA and Centro de Investigaciones Biologicas del Noroeste, La Paz, BCS Mexico

Brander K (2000) Effects of environmental variability on growth and recruitment in cod (*Gadus morhua*) using a comparative approach. Oceanol Acta 23

Campbell JS (1997) Introduction to the Northwest Atlantic Cod Symposium. Can J Fish Aquat Sci 54(Suppl. 1): 1

Christensen V, Pauly D (1998) Changes in models of aquatic ecosystems approaching carrying capacity. Ecol Appl 8 Suppl.: S104-S109

Coombs S, Harris R, Perry I, Alheit J (1998) Globec special issue: foreword. Fish Oceanogr 7: 175

Cushing DH (1995) Population production and regulation in the sea: a fisheries perspective. Cambridge University Press, Cambridge UK

Garrod DJ, Knights BJ (1979) Fish stocks: their life-history characteristics and response to exploitation. Symp zool Soc London 44: 361-382

Gibson RN (1994) Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Neth J Sea Res 32: 191-206

Hay DE, McCarter PB (1997) Continental shelf area and distribution, abundance and habitat of herring in the North Pacific. In: Forage fishes in marine ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant Colleage Program Report No. 97-01. University of Alaska Fairbanks, Fairbanks, Alaska, 559-572

Hennemuth RC, Palmer JE, Brown BE (1980) A statistical description of recruitment in eighteen selected fish stocks. J Northw Atl Fish Sci 1: 101-111

Hilborn R, Walters C (1992) Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York

Hutchings JA (2000) Collapse and recovery of marine fishes. Nature 406: 882-885

Iles TD, Sinclair M (1982) Atlantic herring: stock discreteness and abundance. Science 215: 627-633

Jakobsen T (1996) The relationship between spawning stock and recruitment for Atlantic cod stocks. ICES CM 1996/G:15

Jarre-Teichmann A, Wieland K, MacKenzie B, Hinrichsen H-H, Plikshs M, Aro E (2000) Stock-recruitment relationships for cod (*Gadus morhua callarias* L.) in the central Baltic Sea incorporating environmental variability. Arch Fish Mar Res

Leggett WC, Frank KT (1997) A comparative analysis of recruitment variability in North Atlantic flatfishes - testing the species range hypothesis. J Sea Res 37: 281-299

MacKenzie BR, Hinrichsen H-H, Plikshs M, Wieland K, Zezera A (2000) Quantifying environmental heterogeneity: habitat size necessary for successful development of cod (*Gadus morhua* L.) eggs in the Baltic Sea. Mar Ecol Prog Ser 193: 143-156

Marshall CT, Kjesbu OS, Yaragina A, Solemdal P, Ulltang Ø (1998) Is spawner biomass a sensitive measure of the productive and recruitment potential of the North-east Arctic cod? Can J Fish Aquat Sci 55: 1766-1783

Micheli F (1999) Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. Science 285: 1396-1398

Myers RA (1998) When do environment-recruitment correlations work? Rev Fish Biol Fisheries 8: 285-305

Myers RA (2001) RECENT PAPER IN ICES J OF MAR SCIENCE, I DO NOT HAVE THE REFERENCED WITH ME.

Myers RA, Barrowman NJ (1996) Is fish recruitment related to spawner abundance? Fish Bull 94: 707-724

Myers, RA, Bridson, J, Barrowman, NJ (1995) Summaryof worldwide stock and recruitment data. Can Tech Rep Fish Aq Sci 2024:iv + 327.

Myers RA, Hutchings JA, Barrowman NJ (1996) Hypotheses for the decline of cod in the North Atlantic. Mar Ecol Prog Ser 138: 293-308

Myers RA, Hutchings JA, Barrowman NJ (1997) Why do fish stock collapse? The example of cod in Atlantic Canada. Ecol Appl 7: 91-106

Myers RA, Bowen KG, Barrowman NJ (1999) Maximum reproductive rate of fish at low population sizes. Can J Fish Aquat Sci 56: 2404-2419

Myers RA, MacKenzie BR, Bowen KG, Barrowman NJ (in press) What is the carrying capacity of fish in the ocean? A meta-analysis of population dynamics data from the North Atlantic. Can J Fish Aquat Sci

Myers RA, Mertz G (1998) Reducing uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations: a synthesis. Fish Res 37: 51-60

Planque B, Fredou T (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 56: 2069-2077

Rijnsdorp AD, van Beek FA, Flatman S, Millner RM, Riley JD, Giret M, de Clerck R (1992) Recruitment of sole stocks, *Solea solea* (L.), in the northeast Atlantic. Neth J Sea Res 29: 173-192

Sinclair M, O'Boyle R, Burke DL, Peacock G (1997) Why do some fisheries survive and others collapse? In: Hancock DA, Smith DC, Grant A, Beumer JP (ed) Developing and sustaining world fisheries resources: the state of science and management (2nd World Fisheries Congress). CSIRO Publishing, Collingwood, Australia, 23-35

Sparholt H (1996) Causal correlation between recruitment and spawning stock size of central Baltic cod? ICES J Mar Sci 53: 771-779

Steele JH, Schumacher M (2000) Ecosystem structure before fishing. Fish Res 44: 201-205

Swain DP, Sinclair AF (2000) Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Can J Fish Aquat Sci 57: 1321-1325

Wada T, Jacobson LD (1998) Regimes and stock-recruitment relationships in Japanese sardine (*Sardinops melanostictus*), 1951-1995. Can J Fish Aquat Sci 55: 2455-2463

Watanabe Y, Zenitani H, Kimura R (1995) Population decline of the Japanese sardine *Sardinops melanostictus* owing to recruitment failures. Can J Fish Aquat Sci 52: 1609-1616