

FISH POPULATION REGULATION BEYOND “STOCK AND RECRUITMENT”: THE ROLE OF DENSITY-DEPENDENT GROWTH IN THE RECRUITED STOCK

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ABSTRACT

Most fisheries models are based on the assumption that population regulation occurs exclusively in the prerecruit phase of the life cycle, but increasing evidence indicates that density-dependent body growth in the recruited phase and its interaction with size-dependent reproductive development can play an important role in regulation. I use comparative analyses and population modeling to explore the respective roles in regulation, and the interactions between density-dependent processes in pre- and postrecruit phases of the life cycle. Of 16 study populations, 14 show significant density dependence and therefore regulation in either (9) or both (5) phases. When standardized by habitat area, the density-dependent parameters of both phases are correlated, but the density-dependent growth parameter is a better predictor of average biomass density than the equivalent parameter of the spawner-recruit relationship. Population modeling shows that, in the absence of exploitation (i.e., near carrying capacity), 11 of the 16 populations respond most strongly to relaxation of prerecruit density dependence, whereas 5 respond most strongly to relaxation of density-dependence in postrecruit growth. Growth regulation is less important when population density is reduced below carrying capacity. Fishing erodes compensatory reserve in the recruited phase by truncating the age and size distribution. The spawner-recruit relationship therefore dominates compensation in heavily exploited populations. Growth-mediated regulation in the recruited phase is likely to be important when populations are closer to carrying capacity and therefore particularly relevant to the assessment of harvest reserves, stock rebuilding measures, and fisheries enhancements.

Population regulation is fundamental to the long-term persistence of populations and their responses to harvesting, habitat modification, and other management interventions (Turchin, 1999; Rose et al., 2001). Regulation is effected through density dependence in vital rates (survival, body growth, or reproductive output), which may result from intraspecific competition, predation, or parasitism at various stages of the life cycle. In fisheries ecology, the life cycle of exploited fishes and invertebrates is commonly divided into a prerecruit phase, from spawning to advanced juvenile stage, and a subsequent recruited phase during which the organisms may mature and spawn and are potentially fishable. Spawner biomass is often used as a proxy for egg production, and recruitment is measured in numbers, giving rise to two aggregated “vital rates” that together describe the dynamics of fish populations: recruits per spawner biomass (R/S) for the prerecruit phase and spawner biomass per recruit (S/R) for the recruited phase. Most standard “dynamic pool” fisheries models are based on the assumption that populations are regulated exclusively in the prerecruit stage, through density dependence in R/S . Fish population regulation is thus virtually synonymous with the spawner-recruit (or stock-recruitment) relationship (Ricker, 1954; Beverton and Holt, 1957; Rothschild, 1986, 2000). Increasing evidence, however, indicates that density-dependent processes in the recruited phase can play an

important role in the regulation of fish populations and may need to be considered in management decision making.

An increasingly complex picture of multiple density-dependent processes in the life cycles of fishes has emerged from metaanalyses, experiments, and theoretical studies (Rose et al., 2001). Vital rates of early life stages (eggs and larvae) tend to be highly variable and strongly influenced by environmental conditions but density independent (Myers and Cadigan, 1993b; Leggett and DeBlois, 1994). In contrast, vital rates in juveniles are often density dependent and therefore tend to dampen the variability created at early life stages (Myers and Cadigan, 1993a; Elliott, 1994). Density-dependent survival at this stage may arise directly from density effects on the mortality rate (Elliott, 1994) or indirectly from the interaction of size-dependent mortality with density-dependent growth (Shepherd and Cushing, 1980; Post et al., 1999). Either mechanism or a combination may arise from trade-offs between foraging and predation-risk taking in juveniles and result in density-dependent survival to recruitment (Walters and Korman, 1999; Hixon and Jones, 2005). Ecologically, density-dependence in juvenile survival and the spawner-recruit relationship thus reflects a combination of bottom-up (competition for resources) and top-down (predation) regulation, and the latter is likely to dominate (Munch et al., 2005; Sandin and Pacala, 2005). Density-dependent growth replaces density-dependent mortality as the dominant regulatory mechanism in larger fish, i.e., late juveniles and adults (Walters and Post, 1993; Post et al., 1999; Lorenzen and Enberg, 2002). Density-dependent growth does not immediately regulate numerical abundance but affects population biomass and, in particular, reproductive output through interactions with size-dependent maturation and fecundity schedules. In many fish populations, length at maturity is insensitive to variation in density although the corresponding age at maturity can change substantially as a result of density dependence in growth (Rochet, 1998; Beverton, 2002). Density-dependent growth therefore causes density dependence in S/R . Ecologically, density dependence in growth is directly related to competition for resources, though predation may have a role in restricting habitat use and, thus, resource availability (Walters and Korman, 1999; Hixon and Jones, 2005). The transition from prerecruit mortality to postrecruit growth as dominant regulatory mechanisms in the life history of fish is therefore likely to signify a change from primarily top-down to bottom-up control of abundance (Munch et al., 2005). It also implies a change in the appropriate metric of density, from numerical abundance in juveniles subject to predation to whole-population biomass or similar measures that reflect aggregated effects on resources in adults (Walters and Post, 1993; Lorenzen, 1996).

Although the existence of multiple regulatory mechanisms in fish populations is well established, the importance to population dynamics of processes outside the spawner-recruit relationship has remained controversial. Beverton and Holt (1957) considered density-dependent growth in recruited fish in some detail but concluded that, although important in some populations, the process accounted for a smaller share of overall compensatory reserve than the spawner-recruit relationship. The latter was therefore judged to dominate population responses to exploitation, and the widely used "standard" version of the Beverton and Holt dynamic-pool model thus does not account for density dependence in recruited fish. This omission, together with Ricker's (1954) classic paper on fish population regulation through the spawner-recruit relationship, is likely to explain the almost complete lack of consideration of

other regulatory mechanisms for several decades. Only recently has interest been renewed in the role of regulatory mechanisms in the recruited stage. Lorenzen and Enberg (2002) showed that the density-dependent growth parameter provided a good predictor of long-term average biomass in a sample of 16 fish populations and that regulation by density-dependent growth is sufficient to explain this pattern. Examining the long-term dynamics of 17 fish populations, Rose (2005) concluded that mechanisms “outside the usual spawner-recruit relationship” such as density-dependent growth played an important role in the response to perturbations of some populations. Munch et al. (2005) showed theoretically that bottom-up processes of regulation are likely to limit abundance for a longer period and later in life history than top-down processes, which are largely confined to early life history. Modeling the population dynamics of coral reef fish, Sandin and Pacala (2005) show that although top-down regulation in juveniles suppresses variability in population numbers, bottom-up regulation in adults strongly affects biomass. Empirical evidence and theoretical support are thus increasing for an important role of bottom-up regulation in the recruited stage, mediated by density dependence in growth.

The occurrence of regulatory processes outside the spawner-recruit relationship can have important management implications. The compensatory nature of density-dependent growth implies that, where the process is significant, yield and biomass responses to changes in exploitation are less pronounced than predicted from conventional dynamic-pool models assuming density-independent growth (Beverton and Holt, 1957; Rochet, 2000). Disregarding density-dependent growth would therefore lead to conservative reference points for underexploited stocks but would give rise to overoptimistic assessments of the effectiveness of conservation measures for overexploited stocks (Helser and Brodziak, 1998). In practice, stock reconstruction by catch at age or virtual population analysis often uses annual observations of size and maturity at age and thus accounts for changes in growth and maturity schedules, but the density-dependent element of these changes is not usually quantified and is consequently ignored in predictions. Recent research suggests that density-dependent growth in recruited fish can substantially reduce and possibly eliminate yield biomass gains from spillover from marine reserves that are predicted if density dependence at this stage is ignored (Gårdmark et al., 2006). Explicit consideration of regulation in the recruited phase is particularly important in fisheries stock enhancements, where release of large hatchery fish may effectively circumvent prerecruit density dependence so that responses in the recruited phase determine the ultimate biological limits of enhancement (Peterman, 1991; Lorenzen, 2005).

Here, I address the respective roles in population regulation of density-dependent growth in the recruited phase and density dependence in the spawner-recruit relationship. I do so through a combination of empirical comparative analyses and population modeling.

MATERIALS AND METHODS

I explored the role of density dependence in postrecruit growth and prerecruit mortality in the regulation and dynamics of 16 fish populations. Density-dependent growth and spawner-recruit model parameters were estimated from time series of growth, biomass, and recruitment data. I used two complementary analytical approaches. First, I used regression analysis in among-population comparisons to establish empirical relationships between the

density-dependent parameters in pre- and postrecruit life stages and between the parameters and long-term average population biomass. Second, I used population dynamics modeling to explore the respective roles of density dependence in prerecruit mortality and postrecruit growth in regulation and dynamics of the sample populations by predicting: (1) the effect of relaxing density dependence in either process on equilibrium biomass, (2) the effect of relaxing density dependence in postrecruit growth on temporal variability in biomass, (3) the magnitudes of compensatory responses mediated by both processes. Finally, I explored the impact of fishing on compensatory reserve in the recruited population.

DATA.—Life history information and time series of growth, recruitment, and spawner biomass were assembled for the 16 fish populations (seven freshwater and nine marine) first analyzed by Lorenzen and Enberg (2002). Inclusion in the study was determined by availability of data in the case of freshwater populations; marine populations were a subset drawn at random from exploited populations in the North Sea and adjacent areas. I did not intentionally select populations known to exhibit density-dependent growth, but inadvertent selection cannot be ruled out in the case of freshwater populations, for which data may be more likely to be published if they exhibit ecologically significant patterns. An overview of the sets of data is given in Table 1. Biomass data were based on stock reconstruction from catch-at-age data (by virtual population analysis or related approaches, Hilborn and Walters, 1992) or on direct sampling in the case of some freshwater populations. To allow comparative analyses of density dependence and carrying capacity among populations, I standardized all abundance data by habitat area (this process also results in area-standardized density-dependent parameters). In some cases, per-area densities were measured directly in the field. In other cases, I converted total biomass to standardized density by dividing biomass by the water-body area in the case of lakes and by the relevant statistical area in the case of marine stocks.

MODELS OF DENSITY-DEPENDENT PROCESSES AND PARAMETER ESTIMATION.—Following Lorenzen and Enberg (2002), I described density-dependent growth by a von Bertalanffy growth function with asymptotic length $L_{\infty}(B)$ defined as a linear function of population biomass B :

$$L_{\infty}(B) = L_{\infty L} - gB \quad (1)$$

where $L_{\infty L}$ is the asymptotic length in the absence of competition ($B \rightarrow 0$) and g measures the strength of density dependence. The growth-parameter estimates used here are those obtained by Lorenzen and Enberg (2002). The estimates were obtained by maximum likelihood fitting (with normal error structure) of time series of growth data with biomass density as an explanatory variable. Spawner-recruit relationships were estimated for all 16 populations from time series of spawning-stock biomass and recruitment. Both Beverton-Holt and Ricker spawner-recruit relationships were estimated for all populations, and the best fitting relationship used for comparative analysis and modeling. Both relationships were written so that parameter b describes the negative initial slope of the relationship between R/S and spawning stock biomass (S), i.e., for Beverton-Holt

$$\frac{R}{S} = \frac{a}{1 + bS} \quad (2)$$

and for Ricker

$$\frac{R}{S} = a \exp(-bS) \quad (3)$$

The models were fitted by maximum likelihood with log-normal error structure (Hilborn and Mangel, 1997). Likelihood profiles were used to establish confidence limits and test for significance of the density-dependent parameters (density dependence is statistically significant when the confidence interval does not include zero).

Table 1. Synopsis of studies analyzed. M, marine; F, freshwater.

Study	Species	Location	Source of data
a	Herring, <i>Clupea harengus</i> Linnaeus, 1758	Celtic Sea (M)	ICES (2000a)
b	Herring, <i>Clupea harengus</i>	North Sea (M)	ICES (2000a)
c	Chub, <i>Coregonus hoyi</i> (Gill in Hoy, 1872)	Lake Michigan (F)	Brown et al. (1987)
d	Whitefish, <i>Coregonus lavaretus</i> (Linnaeus, 1758)	Lake Oulujärvi (F)	Salojärvi (1992)
e	Whitefish, <i>Coregonus lavaretus</i>	Lake Inari (F)	Salojärvi and Mutenia (1994)
f	Pike, <i>Esox lucius</i> Linnaeus, 1758	Lake Windermere (F)	Frost and Kipling (1967); Le Cren et al. (1977)
g	Cod, <i>Gadus morhua</i> Linnaeus, 1758	North Sea (M)	ICES (2000b)
h	Haddock, <i>Melanogrammus aeglefinus</i> (Linnaeus, 1758)	North Sea (M)	ICES (2000b)
i	Silver hake, <i>Merluccius bilinearis</i> (Mitchill, 1814)	Gulf of Maine (M)	Ross and Almeida (1986); Helsler and Almeida (1997)
j	Perch, <i>Perca fluviatilis</i> Linnaeus, 1758	Klicava Reservoir (F)	Pivnicka and Svatora (1988)
k	Perch, <i>Perca fluviatilis</i>	Lake Windermere (F)	Le Cren (1958); Le Cren et al. (1977)
l	Flounder, <i>Platichthys flesus</i> (Linnaeus, 1758)	Baltic Sea (M)	ICES (2000c)
m	Plaice, <i>Pleuronectes platessa</i> Linnaeus, 1758	North Sea (M)	ICES (2000b)
n	Roach, <i>Rutilus rutilus</i> (Linnaeus, 1758)	Klicava Reservoir (F)	Pivnicka and Svatora (1988)
o	Sole, <i>Solea solea</i> (Linnaeus, 1758)	North Sea (M)	ICES (2000b)
p	Norway pout, <i>Trisopterus esmarkii</i> (Nilsson, 1855)	North Sea (M)	ICES (2000b)

EMPIRICAL COMPARATIVE ANALYSIS.—Among-population comparisons were used to establish empirical relationships between the density-dependent parameters of postrecruitment growth and prerecruitment mortality and between these parameters and long-term average population biomass density B^* . To facilitate comparisons among populations that differ in asymptotic length, I standardized the density-dependent growth parameter g by $L_{\infty L}$. The new resulting parameter g_s therefore describes the relative decline in asymptotic length per unit of biomass density:

$$g_s = \frac{g}{L_{\infty L}} \quad (4)$$

Regression analysis of logarithmically transformed variables was used for this purpose, and populations with zero or negative point estimates of b or g_s were excluded.

POPULATION MODELING.—A population model was used to explore the role of density-dependence in prerecruit mortality and postrecruit growth in population regulation and dynamics. The model is a standard age-structured fish population model (see, e.g., Hilborn and Walters, 1992) but incorporates density dependence in growth as well as size-dependent maturation and fishing-mortality schedules. Growth is described by the density-dependent von Bertalanffy model defined in Eq. 1, starting with a constant length at recruitment $L(1, t)$. A discrete time model that predicts mean length $L(a, t)$ of age group a at time t from mean length of the cohort in the previous year $L(a - 1, t - 1)$ is given by

$$L(a, t) = L_{\infty}(B) - (L_{\infty}(B) - L(a - 1, t - 1))\exp(-K) \quad (5)$$

where $L_{\infty}(B)$ is the asymptotic length at biomass density B as given by Eq. 1. Population numbers N are given by

$$N(a, t) = N(a - 1, t - 1)\exp(-(F(a - 1, t - 1) + M)) \quad (6)$$

where F is the fishing mortality rate and M is the natural mortality rate.

Fishing mortality is given by a logistic function of length

$$F(a, t) = \frac{F_{\infty}}{(1 + \exp(q(L(a, t) - L_c)))} \quad (7)$$

where F_{∞} is the fishing mortality at fully selected length, L_c is the length at 50% gear selection, and q describes the steepness of the selectivity curve. The proportion mature $Q(a, t)$ is also given by a logistic function of length

$$Q(a, t) = \frac{1}{(1 + \exp(p(L(a, t) - L_m)))} \quad (8)$$

where L_m is the length at 50% maturity and p describes the steepness of the maturity curve.

Total biomass B and spawner biomass S of the population are given by

$$B(t) = \sum_a \alpha L(a, t)^{\beta} N(a, t) \quad (9)$$

$$S(t) = \sum_a Q(a, t) \alpha L(a, t)^{\beta} N(a, t) \quad (10)$$

where α and β are parameters of the length-weight relationship.

Table 2. Synopsis of estimated parameters for the studies analyzed. Long-term average biomass density (B^*); density-dependent von Bertalanffy growth-rate parameter (K), asymptotic length at very low biomass ($L_{\infty L}$) and density-dependent parameter (g); best-fitting spawner-recruit relationship (SRR), either Beverton-Holt (B&H) or Ricker (R); the initial slope (a) and density-dependence (b) parameters of the best-fitting spawner-recruit relationship; residual variance of recruitment ($\text{Var}(R)$); natural mortality rate (M); average fishing mortality rate (F); fishing gear selection length (L_c); and length at maturity (L_m).

Study	B^* (kg ha ⁻¹)	K (yr ⁻¹)	$L_{\infty L}$ (cm)	g (cm ha kg ⁻¹)	SRR	a	b (ha kg ⁻¹)	$\text{Var}(R)$	M (yr ⁻¹)	F (yr ⁻¹)	L_c (cm)	L_m (cm)
a	2.6	0.32	35.8	1.390 [0.970, 1.700]	B&H	9.12	0.236 [0.0, 0.91]	0.21	0.20	0.65	26	26
b	43	0.52	33.0	0.029 [0.002, 0.055]	B&H	15.2	0.059 [0.017, 0.15]	0.49	0.20	0.60	26	24
c	8.8	0.21	53.3	0.378 [0.105, 0.711]	B&H	5.3	0.019 [0.0, 0.41]	3.33	0.40	0.20	18	26
d	0.9	0.54	33.5	3.890 [1.200, 6.500]	R	38.1	3.370 [1.92, 4.88]	0.67	0.40	0.60	24	24
e	2.7	0.32	40.6	1.296 [0.140, 2.240]	R	19.2	1.390 [1.12, 1.67]	0.04	0.40	0.10	24	24
f	4.1	0.33	90.9	1.150 [-0.500, 2.800]	B&H	0.82	0.417 [0.0, 7.7]	0.24	0.30	0.10	60	38
g	9.8	0.23	121.7	0.281 [-0.300, 0.870]	B&H	2.73	0.395 [0.031, 3.33]	0.31	0.20	0.80	35	60
h	20	0.08	94.3	0.000 [-0.260, 0.260]	B&H	53	7.692 [0.14, ∞]	1.28	0.20	0.80	30	32
i	27	0.26	42.5	0.156 [0.070, 0.371]	B&H	4.64	0.008 [0.0, 0.03]	0.49	0.40	0.40	23	23
j	30	0.18	22.6	-0.081 [-0.275, 0.037]	B&H	216	1.926 [0.026, ∞]	0.79	0.30	0.10	13	13
k	119	0.42	23.7	0.028 [0.009, 0.047]	R	108.3	0.049 [0.026, 0.072]	1.44	0.40	0.20	13	12
l	4.3	0.30	38.0	0.490 [-0.550, 1.540]	B&H	3.2	0.125 [0.0, ∞]	0.05	0.20	0.60	25	20
m	8.5	0.07	60.0	-0.350 [-0.580, 0.820]	B&H	61	4.00 [0.22, ∞]	0.28	0.10	0.50	28	29
n	141	0.21	31.9	0.032 [0.013, 0.077]	B&H	1.84	0.00 [0.0, ∞]	0.89	0.25	0.05	13	13
o	1	0.26	44.3	2.791 [1.180, 4.370]	B&H	159	100 [1.92, ∞]	0.63	0.15	0.60	26	26
p	16	0.87	19.8	0.108 [-0.060, 0.280]	B&H	2,603	1.136 [0.04, ∞]	0.40	1.60	0.60	12	16

Recruitment is assumed to occur at age 1 and modeled by the best-fitting Beverton-Holt or Ricker spawner-recruit relationship (see Table 2). Most analyses were carried out with deterministic spawner-recruit models, but a log-normal random error term $\exp(\varepsilon)$ was added to models for Monte-Carlo simulations (see below). The models for recruitment $N(1,t)$ are therefore

$$N(1,t) = \frac{aS(t-1)}{1 + bS(t-1)} \exp(\varepsilon) \quad (11)$$

for Beverton-Holt and

$$N(1,t) = aS(t-1) \exp(-bS(t-1)) \exp(\varepsilon) \quad (12)$$

for Ricker.

To explore the role of pre- and postrecruit density dependence in defining long-term average population biomass, I used the model to predict changes in equilibrium biomass resulting from relaxation of density dependence in the spawner-recruit relationship (setting $b = 0$) or in postrecruit growth (setting $g = 0$). I did so for the 16 sample populations when they were unexploited ($F = 0$) and when they were exploited at their historical average fishing mortality rate.

To establish effects of postrecruit density-dependent growth on variability in biomass, I simulated population dynamics with random variation in recruitment. Log-normal random variation was added to the deterministic spawner-recruit relationships (Eqs. 11 and 12), with variance equal to the residual variance of the estimated spawner-recruit relationships (Table 2).

The magnitude of compensatory responses in R/S to variation in S and in S/R to variation in R was explored with the respective model components. S and R were increased and decreased by 80% relative to the unexploited equilibrium values, and the resulting compensatory responses calculated as relative change in R/S and S/R .

Finally, the demographic effects of fishing on the (growth-mediated) compensatory reserve in S/R were explored, with the North Sea sole population (study o) as an example. Population biomass was reduced from the unexploited equilibrium value by two alternative mechanisms: lowering recruitment in the model (thus reducing biomass without altering population age structure) and exerting different levels of fishing mortality (thus changing age structure by reducing the relative abundance of older fish). These methods permitted comparison of the compensatory reserve conferred by density-dependent growth when populations suffer episodes of low recruitment to that conferred when populations are reduced by fishing (or other sources of high mortality in large fish).

RESULTS

PARAMETER ESTIMATES.—Significant density dependence was detected in body growth of nine (five freshwater and four marine populations) of the 16 study populations (Table 2). Significant density dependence in the spawner-recruit relationship was evident in 10 (four freshwater and six marine) populations. Five populations show significant density dependence in both growth and mortality, nine in just one, and two in neither. Evidence is therefore strong for density dependence in either or both pre- and postrecruitment processes in most populations. Both density-dependent processes occur in freshwater as well as in marine populations, and the data provide no indication of strong associations between regulatory processes and habitat type (freshwater or marine).

COMPARATIVE EMPIRICAL ANALYSIS.—The area-standardized, density-dependent parameters of the growth and spawner-recruit models are correlated (Table 3, Fig.

Table 3. Relationships between the density-dependent growth (g_s) and recruitment (b) parameters and long-term average population biomass (B^*) for the 16 study populations (Table 1). The parameters θ_0 and θ_1 are the intercept and slope of the linear relationships between log-transformed variables. Populations with zero or negative point estimates of g_s or b were excluded.

Model	θ_0 (SE)	θ_1 (SE)	P	rms	n
$\text{Log}(b) = \theta_0 + \theta_1 \text{Log}(g_s)$	1.74 (0.81)	1.09 (0.38)	< 0.02	0.78	12
$\text{Log}(B^*) = \theta_0 + \theta_1 \text{Log}(g_s)$	-1.07 (0.21)	-0.96 (0.10)	< 0.0000001	0.22	13
$\text{Log}(B^*) = \theta_0 + \theta_1 \text{Log}(b)$	0.81 (0.13)	-0.33 (0.12)	< 0.02	0.46	15

1A). Density-dependent processes in the pre- and postrecruit phases therefore would potentially regulate populations toward broadly similar levels of long-term average abundance. The density-dependent growth parameter g_s is a better predictor of average population biomass than the density-dependent recruitment parameter b (Table 3, Figs. 1B and C). This result suggests that density dependence in postrecruit growth either plays an important direct role in or provides a good proxy for processes determining long-term average biomass density (carrying capacity).

ROLE OF GROWTH AND RECRUITMENT REGULATION IN DETERMINING EQUILIBRIUM BIOMASS.—The effects on equilibrium biomass of relaxing density dependence in growth or the spawner-recruit relationship were explored for unexploited populations ($F = 0$, Fig. 2A). The populations exhibit the full range of possibilities, from those responding primarily to relaxation of density dependence in the spawner-recruit relationship to those responding primarily to relaxation in growth regulation. Twelve out of 16 populations showed evidence of regulation by both mechanisms, such that relaxing density dependence in one mechanism resulted in only a limited increase in equilibrium biomass. On average for these populations, relaxing density-dependent growth results in a 2.2-fold increase in equilibrium biomass, whereas relaxing density-dependent recruitment results in a 2.7-fold increase. Both freshwater populations (studies j, f, k, e, d, c, n) and marine populations (studies h, m, o, p, b, l, g, i, a) show the full range of regulatory patterns. The same analysis conducted for populations at their historical average level of exploitation (Fig. 2B) reveals greater responses to relaxing recruitment regulation and lesser responses to relaxing growth regulation. Growth regulation therefore declines in importance when populations are exploited.

IMPACT OF DENSITY-DEPENDENT GROWTH ON VARIABILITY IN POPULATION BIOMASS.—The impact of density-dependent growth on variability in abundance is low to moderate in most of the sample populations but very substantial in four (Fig. 3). Relaxing density-dependent growth causes substantial increases in the variability of populations that either show weak recruitment regulation (populations c, a, and n) or very strong, overcompensating recruitment regulation of the Ricker type (population k).

COMPENSATORY RESPONSES IN R/S AND S/R .—The compensatory responses in R/S to an 80% variation in S exceed the responses in S/R to the same variation in R for most of the sample populations (Fig. 4). Note also that, in many populations, compensation in recruitment is far greater when S is reduced than when S is increased by the same factor. Recruitment thus dominates compensatory responses when population abundance is low relative to carrying capacity, but growth compensation gains in importance when the population is at or above carrying capacity.

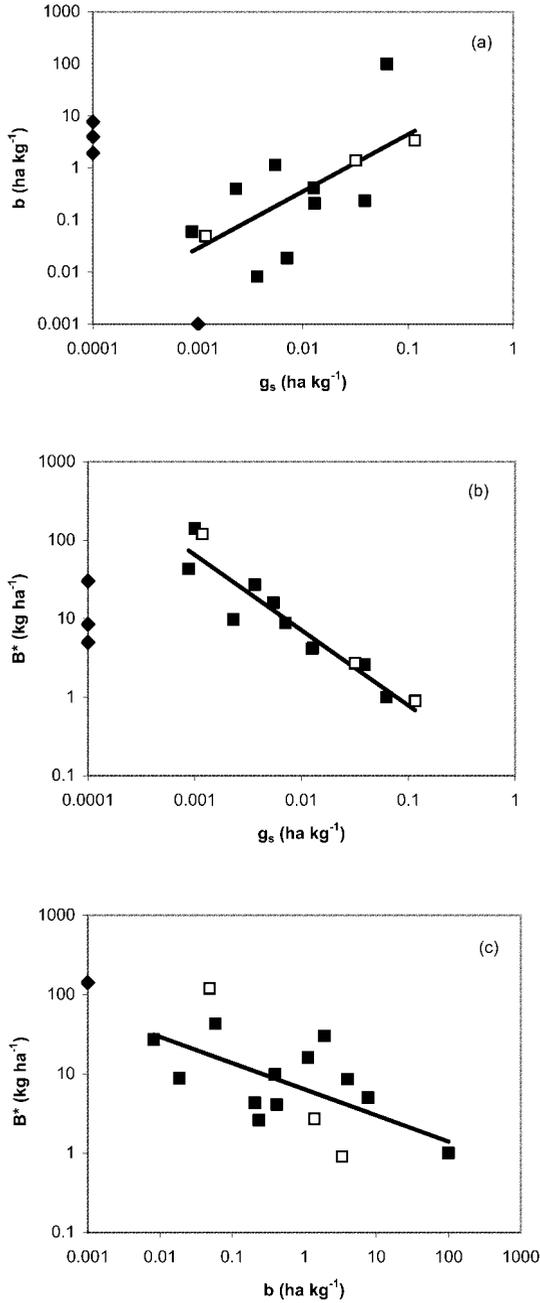


Figure 1. Relationships among the density-dependent standardized growth (g_s) and spawner-recruit (b) parameters and average population biomass (B^*). (A) Relationship between g_s and b . (B) Relationship between g_s and B^* . (C) relationship between b and B^* . Filled squares represent populations with a Beverton-Holt and open squares those with a Ricker stock-recruitment relationship. Data points excluded from the analyses for having point estimates of $b = 0$ or $g_s = 0$ are shown as diamonds on the axes.

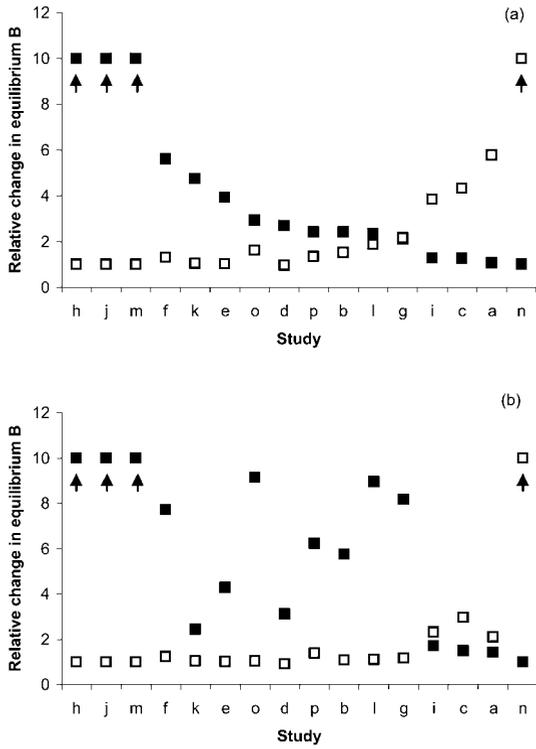


Figure 2. Effects of relaxing density dependence in recruitment (filled squares) or growth (open squares) on equilibrium population biomass, at (A) no fishing and (B) fishing at historical average levels. Populations are ordered by decreasing impact of relaxing density dependence in recruitment (i.e., decreasing degree of recruitment regulation as evidenced by this response).

DEMOGRAPHIC EFFECTS OF FISHING ON COMPENSATORY RESERVE.—Growth-mediated compensatory responses in S/R to a decrease in population abundance vary according to the cause of the decrease (Fig. 4). A decrease in abundance due to low recruitment elicits a stronger compensatory response than a reduction to the same biomass by fishing. The reason lies in the different demographic impacts of these causes of population reduction. Low recruitment does not affect the proportion of old and large fish in the population in the long run and may increase it temporarily. Fishing on the other hand reduces the proportion of old and large fish. Large fish play a particularly important role in growth-mediated compensation, and fishing therefore erodes this component of the compensatory reserve of fish populations.

DISCUSSION

Empirical comparative analysis and population modeling have produced a number of new insights into the importance of density-dependent growth in the recruited phase in fish population regulation and its relation to regulation in the spawner-recruit relationship. Perhaps the most important of these is that variation is tremendous with respect to the importance of regulation at different life stages, both among populations and within populations for different levels of abundance. This result alone suggests that fisheries ecology should broaden its paradigm of population reg-

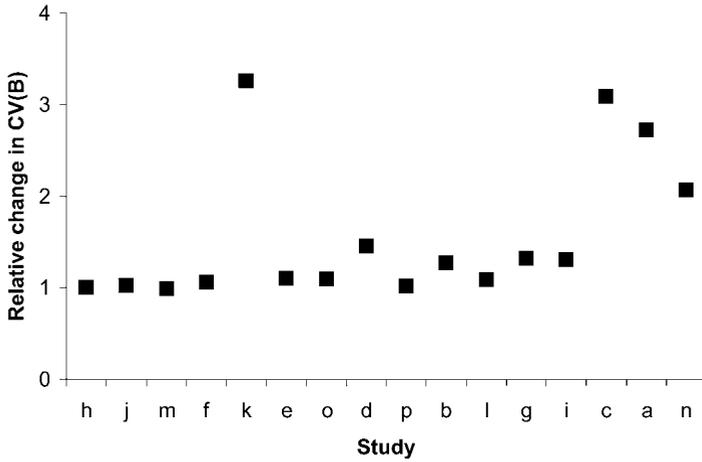


Figure 3. Change in the coefficient of variation of population biomass when density dependence in growth is removed, at historical average levels of fishing mortality. Simulations were stochastic, with recruitment variability at observed historical levels.

ulation and recognize that some populations may be strongly influenced by regulatory processes outside the spawner-recruit relationship (see also Rose and Cowan, 2000; Rose, 2005). It also implies that populations that do not show strong density dependence in the spawner-recruit relationship should not automatically be regarded as weakly regulated: regulation may simply be dominated by other processes such as growth in the recruited stage, as is the case in several of the populations studied here: silver hake (i), chub (c), Celtic Sea herring (a), and roach (n). Among-population variation in regulatory mechanisms is perhaps not surprising, given that in many fish populations different life stages depend on different habitats that may vary in

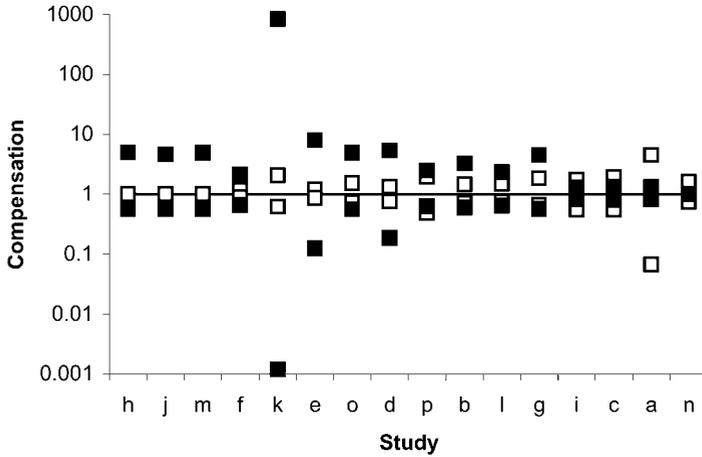


Figure 4. Compensatory response in recruits per unit spawner biomass (R/S , filled squares) and spawner biomass per recruit (S/R , open squares) to an 80% variation in S and R respectively. Compensatory response is expressed as change relative to the value at unexploited equilibrium S or R . Values greater than one show responses to a reduction in S or R , whereas values less than one show responses to an increase.

their carrying capacity such that overall regulation is likely to be strongest in the most limiting habitat and associated life stage. On the other hand, extreme differences such that relaxing density-dependence in the most strongly regulated life stage would allow the population to expand by an order of magnitude or more do not appear to be the norm. I found no indication of strong associations between regulatory pattern and habitat (freshwater or marine), but the current sample of populations is too small to allow systematic testing of such associations.

Despite the level of variation among populations, several broad generalizations can be made about the importance of growth-mediated regulation in the recruited phase vis-à-vis regulation through the spawner-recruit relationship. Most populations exhibit evidence of regulation at both stages. The predictive power of the density-dependent growth parameter for long-term average biomass density suggests that the postrecruit density-dependent growth either plays an important direct role in or provides a good proxy for processes determining carrying capacity. Population dynamics modeling shows that, although only 5 out of the 16 populations are primarily growth-regulated even under unexploited conditions, most (13 out of the 16) populations show evidence of some level of growth regulation. Relaxing one regulatory mechanism on average only led to a limited increase in predicted equilibrium biomass (by a factor of 2.2–2.7). Within populations, the relative contribution of the different mechanisms often changed with population abundance: the spawner-recruit relationship conferred the greatest compensatory reserve when populations were depressed below carrying capacity, but growth in the recruited phase became increasingly important as the population approached or exceeded carrying capacity. This result suggests that growth in the recruited phase plays an important role in determining carrying capacity, a conjecture also supported by the role of the density-dependent growth parameter as a good predictor of long-term average biomass. Interestingly, a similar pattern of change in the importance of regulatory processes, from juvenile survival to adult reproductive rates as abundance approaches carrying capacity, has been observed in mammals (Eberhardt, 2002).

The impact of fishing on compensatory reserve in the recruited phase is worthy of further analysis. This effect (shown in Fig. 5) arises because old and large fish show the largest absolute growth response to changes in population biomass, yet their relative abundance is greatly reduced by fishing. The resulting loss of growth-mediated compensatory reserve is separate from other, previously noted impacts of changes in population age structure caused by fishing (see Longhurst, 2002; Beamish et al., 2006).

An important implication of these results for fisheries management is that the spawner-recruit relationship is likely to capture the most important compensatory response in populations that are heavily exploited. This conclusion reflects both the high compensatory reserve immanent in many spawner-recruit relationships at low spawner biomass and an erosion of compensatory reserve in the recruited phase due to the demographic impact of fishing. The focus of fisheries ecology on exploited populations and its reliance on fisheries data may thus explain why regulatory mechanisms outside the spawner-recruit relationship have received so little attention in the discipline, but the current results suggest that regulation in the recruited phase is an important consideration where populations approach their natural carrying capacity, for example in marine reserves or under stock rebuilding or enhancement measures (Helser and Brodziak, 1998; Lorenzen, 2005; Gårdmark et al., 2006).

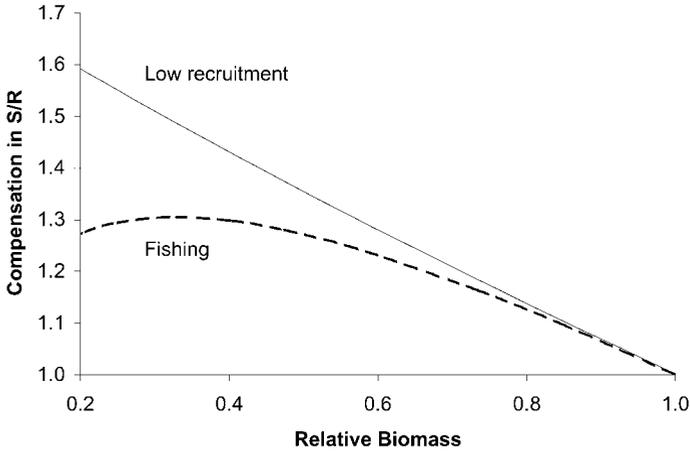


Figure 5. Compensatory response in S/R to a decrease in total population biomass caused by low recruitment or by fishing, for the North Sea sole population. Fishing changes population age structure and reduces the compensatory reserve conferred by density-dependent growth.

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