

Correlates of recovery for Canadian Atlantic cod (*Gadus morhua*)¹

Jeffrey A. Hutchings and Robert W. Rangeley

Abstract: The collapse of Atlantic cod (*Gadus morhua* L., 1758) in the early 1990s, perhaps the greatest numerical loss of a Canadian vertebrate (1.5–2.5 billion reproductive individuals), is one from which the species has yet to recover. Populations, or stocks, are at or well below their conservation reference points. The lack of recovery has been linked to ongoing fishing mortality (targeted, bycatch), changes to life history (reductions in age and size at maturity, truncations in age and size structure), and increased natural mortality. Emergent and demographic Allee effects, coupled with altered interspecific interactions, render questionable the presumption that the recovery of heavily depleted populations can be reliably forecasted by population dynamical behaviour during decline. Contrary to international commitments and inconsistent with fishery rebuilding plans elsewhere, cod recovery plans exclude target and limit reference points, recovery timelines, and harvest control rules. We suggest that the long-term biodiversity, social, and economic benefits associated with cod recovery can be realised by novel changes, including quantitatively responsible recovery plans based on science-determined reference points, new or revised legislation, integrated management strategies, strengthened sustainable seafood certification practices, expansion of marine spatial planning and protected areas, and novel financial incentives for investment in long-term, sustainable fisheries.

Résumé : L'effondrement des populations de morues (*Gadus morhua* L., 1758) au début des années 1990, peut-être la plus grande perte numérique de vertébrés au Canada (1,5–2,5 milliards d'individus reproducteurs), est un événement dont l'espèce ne s'est pas encore remise. Les populations, ou stocks, sont au niveau de leur points de référence de conservation ou à un niveau bien inférieur. L'absence de récupération a été expliquée par une mortalité persistante due à la pêche (pêche ciblée, captures accessoires), par des changements dans le cycle biologique (réduction de l'âge et de la taille à la maturité, structures en âge et en taille tronquées) et par une mortalité naturelle accrue. Des effets émergents et des effets démographiques d'Allee, associés à des modifications des interactions interspécifiques, remettent en question la présupposition que le rétablissement de populations fortement décimées peut être prédit avec assurance à partir du comportement de la dynamique de population durant le déclin. Contrairement à nos engagements internationaux et en désaccord avec les plans de récupération de la pêche utilisés ailleurs, nos plans de récupération de la morue excluent les points de référence cibles et limites, les calendriers de récupération et les règles de contrôle de la récolte. Nous croyons que les bénéfices à long terme en ce qui concerne la biodiversité, la vie sociale et l'économie associés au rétablissement des populations de morues peuvent être réalisés par des changements ingénieux, en particulier des plans de récupération sérieux et quantitatifs basés sur des points de référence déterminés de manière scientifique, une législation nouvelle ou renouvelée, des stratégies de gestion intégrées, des pratiques améliorées et durables de certification des fruits de mer, une expansion des la planification spatiale marine et des zones protégées et de nouveaux stimulants financiers pour un investissement à long terme dans une industrie durable de la pêche.

[Traduit par la Rédaction]

Received 19 September 2010. Accepted 18 February 2011. Published at www.nrcresearchpress.com/cjz on 27 April 2011.

J.A. Hutchings. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

R.W. Rangeley. WWF Canada, Atlantic Region, 1202-5251 Duke Street, Halifax, NS B3J 1P3, Canada.

Corresponding author: J.A. Hutchings (e-mail: jhutch@mathstat.dal.ca).

¹This review is part of the virtual symposium “Flagship Species – Flagship Problems” that deals with ecology, biodiversity and management issues, and climate impacts on species at risk and of Canadian importance, including the polar bear (*Ursus maritimus*), Atlantic cod (*Gadus morhua*), Piping Plover (*Charadrius melodus*), and caribou (*Rangifer tarandus*).

Introduction

Systems must be stressed before their strengths and weaknesses are fully known. The decline of many marine fishes at multiple spatial and temporal scales has exacted considerable stress for those responsible for the exploitation and conservation of marine resources and increased scrutiny of the regulatory, policy, and legislative frameworks under which these responsibilities are exercised. Although commercially exploited marine fishes in some regions (e.g., Northeast Pacific, Australia, New Zealand) are comparatively healthy (Worm et al. 2009; Hutchings et al. 2010), many elsewhere are not. Since 1970, based on fisheries stock assessment data, it is estimated that marine fish abundance has declined 38% globally and that the rate of decline among top predators has increased since 1992 (Hutchings et al. 2010). On a positive note, fishing mortality (F) appears to have declined sufficiently in 5 of 10 well-studied ecosystems to permit rebuilding of depleted populations (Worm et al. 2009). The key question now is whether the reductions in F , while clearly being necessary, will be sufficient to effect recovery. This question is particularly germane for marine fishes in the Northwest Atlantic basin, and especially so for Canadian populations of Atlantic cod (*Gadus morhua* L., 1758).

Now is an appropriate time to examine efforts to recover cod in Canadian waters. Firstly, the United Nations declared 2010 to be the International Year of Biodiversity in recognition of an objective articulated by the Convention on Biological Diversity to achieve by 2010 a significant reduction of the current rate of biodiversity loss (<http://www.cbd.int/2010-target/about.shtml>; accessed 30 March 2011). Secondly, Canada is one of many signatories to the 2002 Johannesburg World Summit on Sustainable Development agreement to “maintain or restore [fish] stocks to levels that can produce the maximum sustainable yield with the aim of achieving these goals for depleted stocks on an urgent basis and where possible not later than 2015” (<http://www.johannesburgsummit.org>; accessed 30 March 2011). Thirdly, Canada’s national arms-length-from-government federal advisory body on species at risk—COSEWIC (Committee on the Status of Endangered Wildlife in Canada)—recently (2010) communicated its advice to the federal Minister of Environment on the current status of Atlantic cod (its third assessment in 12 years), providing a metric of whether the species’ status has improved or deteriorated over time. Fourthly, the Canadian government’s continual rejection of COSEWIC’s advice to list an Endangered or Threatened marine fish under Canada’s *Species At Risk Act* (SARA; with the 2010 exception to list the commercially unexploited basking shark, *Cetorhinus maximus* (Gunnerus, 1765), in the Pacific) raises questions as to whether the existing legislative framework is one best suited for the conservation management and rebuilding of depleted marine fish populations, such as cod. The time may be opportune to offer solutions and suggestions that would strengthen Canada’s ability to fulfil its national and international obligations to recover and conserve marine biodiversity.

The thread linking the topics covered here is that of conservation biology, which we define to encompass those factors that influence realised per capita population growth rate (r) at low levels of abundance. This definition includes both

natural and anthropogenic sources of mortality and stochastic sources of variability in age-specific schedules of survival and fecundity attributable to demographic, environmental, and genetic stochasticity (Lande 1993).

Overall, our intention is to provide a broad contextual framework in which to consider various factors that are likely to affect the recovery of Canadian Atlantic cod. Beginning with a brief historical perspective, we describe the current status of cod in Canadian waters, using data on temporal trends in abundance and life history. We then consider how changes to life history and population dynamics can affect prospects for recovery before underscoring what we perceive to be the utility—indeed the necessity—of developing quantitatively explicit fishery management plans that formally acknowledge and utilize science-determined (as opposed to science-based) reference points. Among other considerations, and within the context of Canada’s commitments to conserve biodiversity, we explore the question of whether current management measures, policies, and legislation are sufficient to permit recovery, growth, and long-term sustainable harvesting of Atlantic cod. Finally, we examine how consumer demand for sustainable seafood has influenced the fishing industry and how this phenomenon, combined with innovative financing instruments, can positively affect marine conservation and cod recovery.

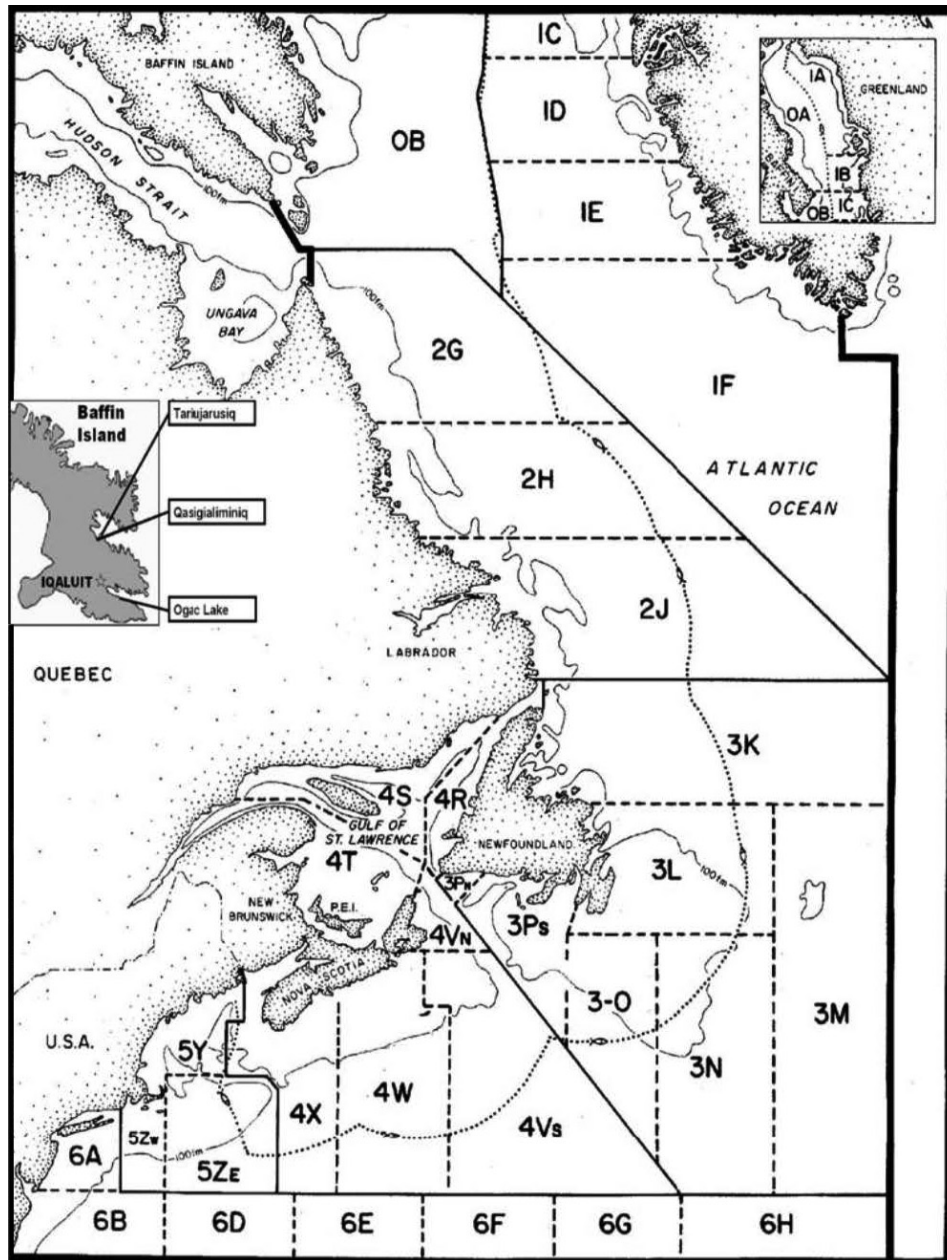
Status of Canadian Atlantic cod

Historical context: Northern cod

The largest cod population in Canadian waters (an estimated 70% of Canadian cod spawning stock biomass or SSB in 1962; COSEWIC 2010), and once the largest in the world in terms of SSB (Hutchings and Myers 1994), was that comprising Northern cod, extending from southern Labrador (55°20′N) southeasterly along the Northeast Newfoundland Shelf to include the northern half of the once biologically rich Grand Bank (46°00′N). Northern cod is delineated for management purposes by Northwest Atlantic Fishery Organization (NAFO) divisions 2J (Southern Labrador), 3K (Northeast Newfoundland Shelf), and 3L (Northern Grand Bank) (Fig. 1).

Cod have probably been fished by Europeans in Canadian waters since the late 15th century, although the earliest extant documentation of a Newfoundland fishery dates from 1504 (Hutchings and Myers 1995; Rose 2007). Total harvests of northern cod appear to have been less than 100 000 t (tonne or Metric ton) until the late 18th century whereupon catches increased to as much as 300 000 t in the 1880s and 1910s before declining to less than 150 000 t in the mid-1940s (Fig. 2). Following the expansion of European-based factory trawlers in the late 1950s and early 1960s, particularly in the virtually unfished offshore waters off southern Labrador, reported catches increased dramatically to a historical maximum of 810 000 t in 1968 before collapsing in equally dramatic fashion by 1977 when Canada extended its exclusive economic zone, and thus its fisheries jurisdiction, to 200 nautical miles (1 nautical mile = 1.852 km). Controlled in part by quotas established by the newly formed Canadian Department of Fisheries and Oceans (DFO; currently Fisheries and Oceans Canada), catches of northern cod increased gradually to a post-1977 high of 268 000 t in 1988 before the

Fig. 1. Map showing the Northwest Atlantic Fishery Organization (NAFO) alphanumeric divisions used to delineate the fisheries management boundaries of commercially exploited marine fishes, including Atlantic cod (*Gadus morhua*).



imposition of a moratorium on directed commercial fishing in July 1992.

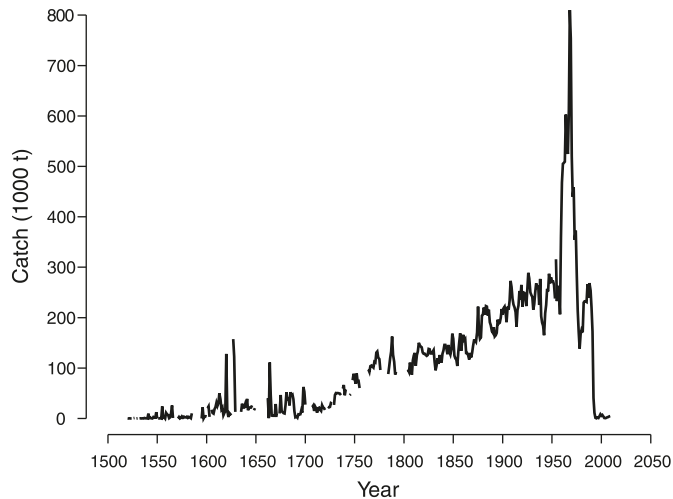
Although the 1992 moratorium significantly curtailed fishing activity, the catching of cod did not end. The median annual reported catch of northern cod from 1993 to 2009 from all sources was 2918 t (DFO 2010a). During this period, cod were caught mainly, although not entirely (because of incidental catches), in inshore waters as a result of the following: directed fisheries; bycatch (inshore and offshore); food and recreational fisheries; a DFO-industry sentinel survey (that began in 1995); and illegal exploitation. A directed commercial fishery for northern cod was re-opened in 1998 (for inshore waters only). The catches and associated levels of fishing mortality that ensued (DFO 2003), until this fishery

was closed from 2003 to 2005, served to retard recovery (Hutchings and Reynolds 2004). A directed fishery for northern cod in inshore waters (and a recreational fishery) was re-opened in 2006 and continues today. The 1992 fishing moratorium for northern cod in offshore waters was still in place by the beginning of 2011.

Collapse of Canadian Atlantic cod

To place the decline of the species in some context from a conservation perspective, the collapse of Atlantic cod almost certainly represents the greatest numerical loss of a vertebrate species in Canada, representing a reduction of between 1.5 and 2.5 billion breeding individuals (assuming an mean mass of reproductive cod between 800 and 1330 g (Lilly

Fig. 2. Catches of northern Atlantic cod (*Gadus morhua*) from the early 16th Century to the present. Data prior to 1962 are those presented by Hutchings and Myers (1995). Data from 1962 to 2008 are those from Bratley et al. (2009).



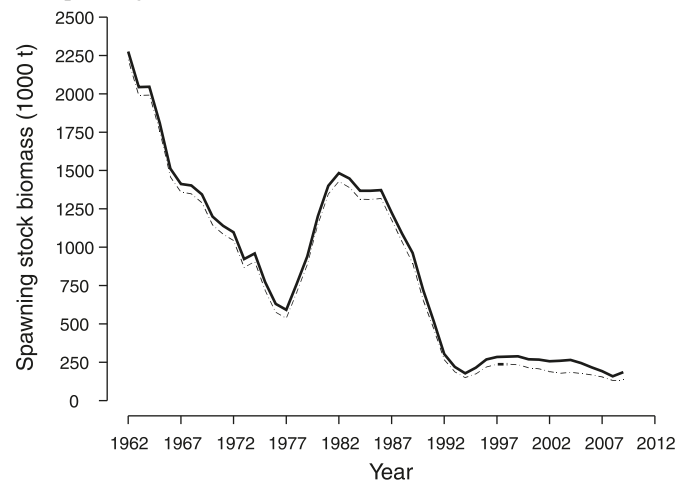
1997) and a loss of at least 2 million tonnes). Between 1962 and 1992, Canadian cod as a whole are estimated to have declined more than 90% (Fig. 3).

The collapse of cod in the early 1990s has been the subject of numerous publications (e.g., Hutchings 1996; Myers et al. 1997a; Drinkwater 2002; Rose 2004; Lilly et al. 2008; Hilborn and Litzinger 2009), beginning with those on Northern cod that proffered the hypotheses that declining water temperatures (deYoung and Rose 1993) or excessive fishing pressure (Hutchings and Myers 1994) were primary drivers of the stock's collapse. Although reduced individual growth rates in some areas, possibly increased predation in other areas, and declining body condition in yet other areas may also have been contributing factors, the scientific consensus would appear to be that these influences compounded the effects of overexploitation, rather than being of singular importance to population decline in and of themselves (Lilly et al. 2008).

Notwithstanding the massive employment, societal, and economic losses associated with the collapse of cod, the numerical reduction of the species represented an unprecedented change in Canadian marine biodiversity (DFO 2010b; Templeman 2010). Perhaps the most demonstrable consequence of these altered ecosystems was an increase in prey that were once heavily preyed upon by cod, such as shrimp (*Pandalus borealis* Krøyer, 1838) and snow crab (*Chionoecetes opilio* (J.C. Fabricius, 1788)) (Worm and Myers 2003).

There are concerns that fishery-induced changes to predator-prey interactions may significantly retard, or even prevent, the recovery of depleted populations. One potential example is that provided by cod in the Southern Gulf of St. Lawrence (the SSB of this stock was greater than that of Northern cod in the mid-1980s; Figs. 4, 5) which have declined to such low levels, and are experiencing such high levels of natural (non-fishing) mortality, that they are predicted to become effectively extirpated by 2050 (Swain and Chouinard 2008). One factor originally thought to be inhibiting their recovery is the increase in abundance of species, such as Atlantic mackerel (*Scomber scombrus* L., 1758) and her-

Fig. 3. Estimated spawning stock biomass (SSB) of Canadian Atlantic cod (*Gadus morhua*) from 1962 to 1998. Data are included for cod inhabiting waters from southeastern Labrador to the Canadian portion of Georges Bank (approximately 150 km from southwestern Nova Scotia), i.e., Northwest Atlantic Fishery Organization (NAFO) divisions 2J3KLNOPRS4TVWX5YZj,m. Estimates of SSB are available for cod in the following Northwest Atlantic Fishery Organization divisions: 2J3KL (Baird et al. 1991; DFO 2010a); 3NO (Power et al. 2010); 3Ps (DFO 2009a); 3Pn4RS (DFO 2010c); 4T (DFO 2009b); 4VsW (Worcester et al. 2009); 4X/5Y (DFO 2009c); 5Zj,m (COSEWIC 2010). Estimates for some populations do not extend to 1962. For these stocks, annual estimates of SSB were set to the medians for all available data for each population. Note that two lines are shown in the figure to reflect the fact that two time series of SSB have been reported for St. Pierre Bank cod (NAFO division 3Ps; DFO 2009a). These medians (in tonnes, t, and the years in which they were used in the time series are as follows: 3Ps (23 400 and 78 000 t; 1962–1978); 3Pn4RS (45 638 t; 1962–1973); 4X/5Y (32 467 t; 1962–1979); 5Zj,m (22 681 t; 1962–1977). These medians sum to a total of less than 8% of the estimated total cod spawning biomass in 1962.

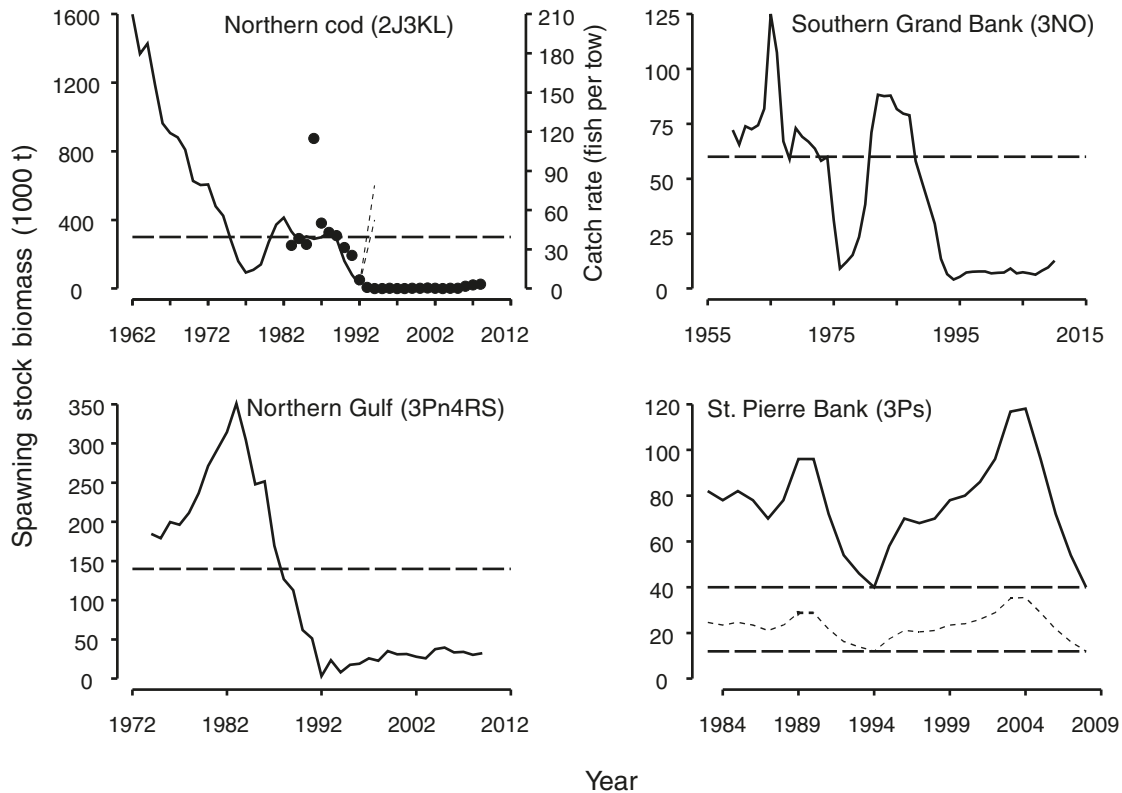


ring (*Clupea harengus* L., 1758), that prey upon cod eggs and larvae (and potentially compete with larval and juvenile cod) (Swain and Sinclair 2000). In addition to this hypothesized negative influence on cod recruitment, a second factor increasingly thought to be responsible for the increased mortality of Southern Gulf cod is predation by grey seals (*Halichoerus grypus* (Fabricius, 1791)) (DFO 2011a; Swain 2011).

Trends in abundance and life history

In 2010, COSEWIC assessed all Canadian cod south of Hudson Strait as Endangered (those inhabiting Baffin Island lakes (Hardie and Hutchings 2011) were assessed as Special Concern). This assessment was considerably more pessimistic than those undertaken by COSEWIC in 1998, when all populations were as assessed as Special Concern, and in 2003, when only one population was assessed as Endangered. In 2005, the Canadian government rejected COSEWIC's 2003 advice to add Endangered and Threatened cod populations to the national legal list of species at risk. The most recent available data indicate that cod are either at (St. Pierre Bank cod) or well below (all others) their conservation reference points (Figs. 4, 5), i.e., the SSB below which productivity,

Fig. 4. Temporal changes in the estimated spawning stock biomass (SSB) of four Canadian populations of Atlantic cod, *Gadus morhua* (the Northwest Atlantic Fishery Organization divisions encompassing each population are indicated in parentheses; see caption to Fig. 3 for data sources of SSB estimates). For Northern cod, the short dashed lines represent the projected 1992–1994 increases in SSB predicted by Department of Fisheries and Oceans (DFO) currently Fisheries and Oceans Canada) in 1992; the circles represent the catch rate (number of fish per tow) of cod aged 5 years and older obtained by the DFO's fisheries-independent survey in offshore waters. For St. Pierre Bank cod, the two trends represent the high and low estimates of SSB provided by DFO (2009a). The long horizontal dashed lines in each panel represent the limit reference points defined by DFO stock assessment scientists for Northern cod (DFO 2005a), Southern Grand Bank cod (Power et al. 2010), St. Pierre Bank cod (DFO 2009a), and Northern Gulf cod (DFO 2010a).



and thus recovery potential, is likely to be significantly impaired.

Although the recent trajectory of most cod populations has exhibited either stability or further decline (Figs. 4, 5), that for Northern cod in offshore waters has been increasing. From 2004 to 2008, SSB is estimated to have increased to 8% of levels observed in the 1980s (DFO 2010c). However, placed within a broader and arguably more appropriate temporal context, the current SSB of Northern cod is approximately 2%–3% of the SSB estimated for the stock in the early 1960s, when it was quite possibly at, or close to, the biomass at which maximum sustainable yield would be predicted to have been obtained (Hutchings and Myers 1995; Hilborn and Litzinger 2009). There is evidence that the SSB for this population has levelled off (in 2009) and it has been forecasted that relatively weak incoming year classes will limit further increases in SSB in the short term (DFO 2010c). Concern has also been expressed that some spawning components may have become extirpated, e.g., Virgin Rocks (DFO 2011b), the long-term consequences of which to recovery and persistence are not known.

Concomitant with reductions in abundance have been significant changes in life-history traits (Trippel et al. 1997; Olsen et al. 2005; Bratney et al. 2008; Fudge and Rose 2008). Prominent among these are reductions in age at maturity.

Year

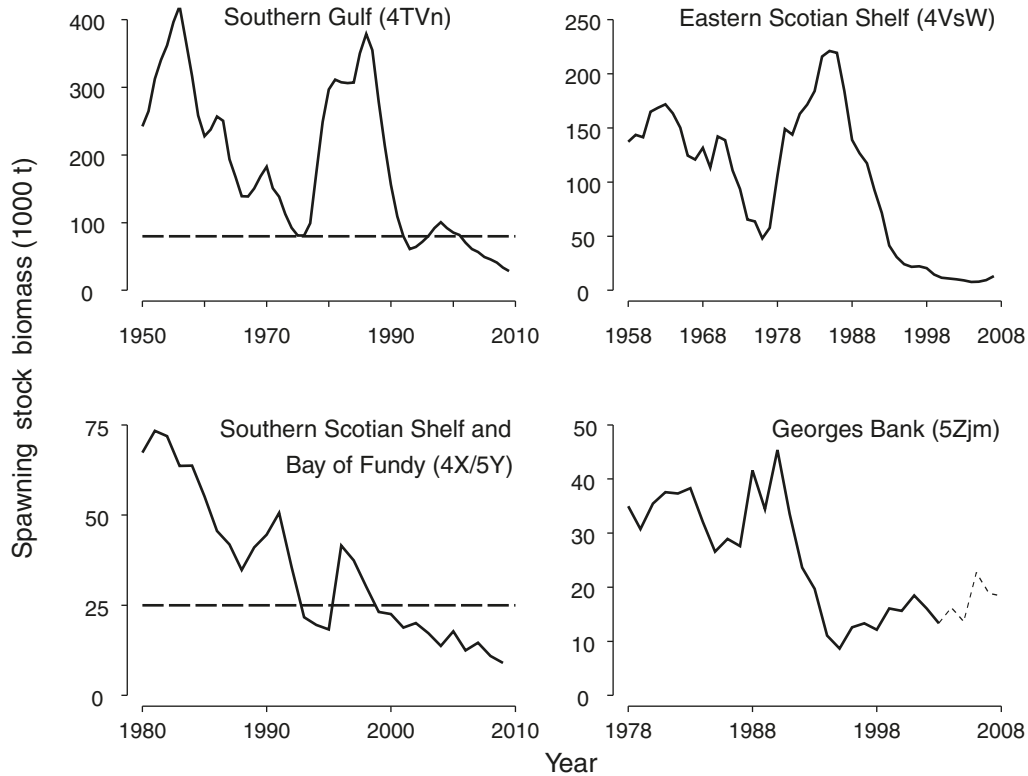
For at least four populations, the age at which the probability of maturity is 50% has declined between 2 and 3 years over the past 5–6 decades (Fig. 6). Within some populations, reductions in size at maturity have also been substantive. Length at maturity among Eastern Scotian Shelf cod, for example, declined from approximately 42 cm in the late 1970s to 32 cm in the early 2000s (Fanning et al. 2003; Hutchings 2005). Population growth rate and, thus, recovery are affected by changes to life history (e.g., Cole 1954; Roff 1984). Earlier age at maturity, smaller size at maturity, and truncated distributions in age and size at maturity can, to varying degrees, be expected to negatively affect r as a consequence of higher post-reproductive mortality, reduced life span, lower fecundity, smaller egg size, and increased temporal variability in offspring survival (Beverton et al. 1994; Hutchings 1999, 2005; Venturrelli et al. 2009; Jørgensen and Fiksen 2010).

Recovery: Considerations of life history and population dynamics

A species less able to hedge its bets?

Environments vary to greater or lesser degrees across all spatial and temporal scales. The less predictable the environment, the greater the selective pressures to evolve a life history that spreads the risk of reproductive failure across space

Fig. 5. Temporal changes in the estimated spawning stock biomass (SSB) of four Canadian populations of Atlantic cod, *Gadus morhua* (the Northwest Atlantic Fishery Organization divisions encompassing each population are indicated in parentheses; see caption to Fig. 3 for data sources of SSB estimates). The long horizontal dashed lines in each panel represent the limit reference points defined by DFO stock assessment scientists for Southern Gulf cod (DFO 2009b), and Southern Scotian Shelf and Bay of Fundy cod (DFO 2009c). The SSB estimates represented by a short dashed line for Georges Bank cod from 2004 to 2008 represent the output resulting from a log–log regression between SSB and fisheries-independent survey catch rates for cod aged 3 years and older, for which data were available from 1978 to 2003 (Worcester et al. 2009).



or time. Under such circumstances, selection is expected to act against genotypes whose life histories have them placing “all their eggs in one basket”. That is, selection should act to reduce the variance in genotypic or individual fitness over generations, even if this entails a “sacrifice” of the expected fitness within any one generation (Roff 2002).

Life histories such as these are termed bet-hedging strategies (Childs et al. 2010). Bet-hedgers spread their reproductive risks over time by reproducing multiple times throughout their lives, multiple times in a single breeding season, and (or) multiple times within the same breeding location (almost always with multiple mates, spreading the risk even farther). Natural selection has clearly favoured the evolution of a bet-hedging life history in Atlantic cod (and other marine fishes; Roff 1981), a species in which (i) females release eggs in multiple batches (usually every 4–7 days) during a single breeding season; (ii) males and females breed with multiple mates in a single season; and (iii) spawning occurs annually or biannually during a reproductive life span (in unfished populations) likely to encompass 15–20 years (Kjesbu 1989; Rowe et al. 2008).

When establishing management recovery targets, it is fundamentally important to consider how fishery-induced truncations in reproductive life span, in addition to reductions in age and size at maturity, will affect the ability of cod to hedge its bets against natural and anthropogenic environmen-

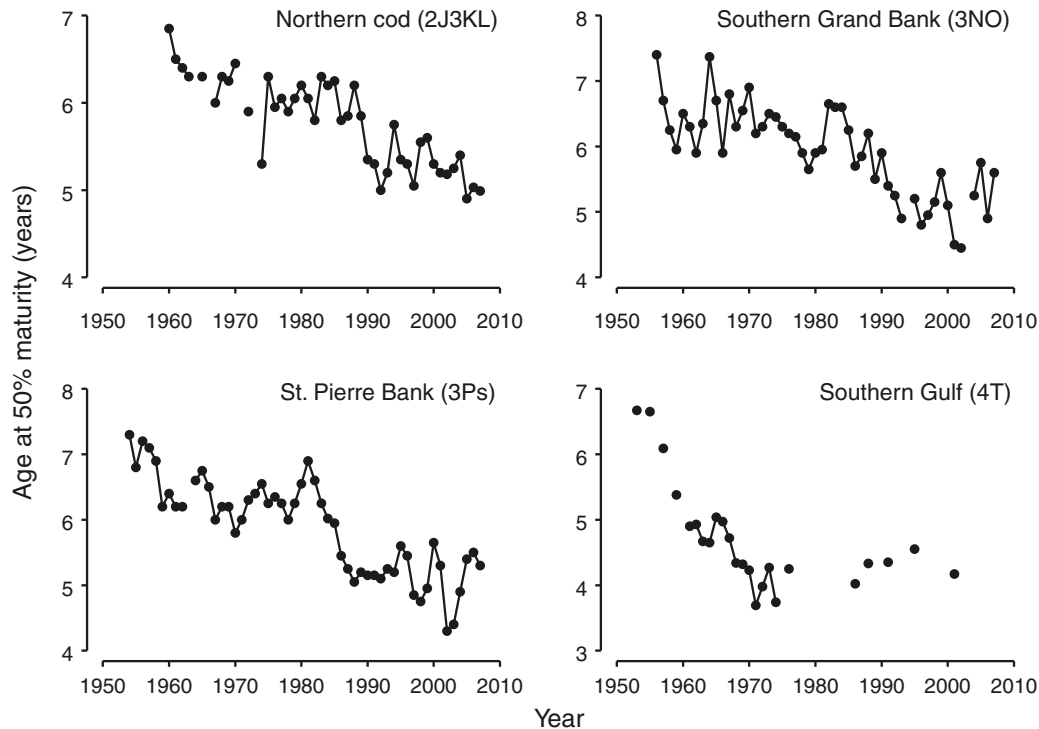
tal stochasticity. All depleted cod populations have, to varying degrees, experienced significant truncations in their age and size distributions. Northern cod provide an illustrative example. The contribution of eggs by cod 10 years and older to the population is estimated to have declined from an annual mean of 30% in the 1960s (46% in 1962) to 17% in the 1970s and 12% in the 1980s (Hutchings and Myers 1994). Their low incidence in fishery and survey catches (Bratley et al. 2009) suggests that cod 10 years and older have contributed a negligible proportion of eggs to the population since 1992.

Stock-recruitment models implicitly assume that a tonne of spawning stock biomass produces the same level of recruitment (and variance thereof) irrespective of the age or size of individuals that comprise that tonne of SSB. Although the question of whether recruitment, and potentially r , is affected by the breadth of the age and size classes of the spawning population has received comparatively little attention, there are theoretical (Hutchings and Myers 1993) and empirical reasons (Vallin and Nissling 2000; Berkeley et al. 2004; Venturelli et al. 2009) for believing that a positive association may well exist.

Reproductive value

One means of evaluating the relative importance of age (and indirectly size) to population growth is to quantify the

Fig. 6. Reductions in age at 50% maturity in four Canadian Atlantic cod (*Gadus morhua*) stocks: Northern cod (Brattey et al. 2009); Southern Grand Bank (Power et al. 2010); St. Pierre Bank (Brattey et al. 2008); and Southern Gulf of St. Lawrence (Swain 2011).



reproductive value (Fisher 1930; Williams 1966). Reproductive value at age, V_x , represents the present and future production of offspring by an individual breeding at age x and living through to its maximum possible life span (i.e., to age $x = \omega$), discounted by the probability of that individual surviving to its maximum possible age. It can be calculated as

$$V_x = \sum_{t=x}^{\omega} \frac{l_t m_t}{l_x}$$

where l_t and m_t represent the age-specific schedules of survival and fecundity, respectively. For northern cod, reproductive value is estimated to be initially low, but to increase to a maximum value near age 15, before declining once again (Fig. 7), suggesting that older cod (e.g., 14- and 15-year-olds) are the most valuable to future population growth, a prediction borne out by recent reports that marine fishes consisting of older, larger individuals have higher r_{\max} than an equivalent population of younger, smaller individuals (Venturelli et al. 2009).

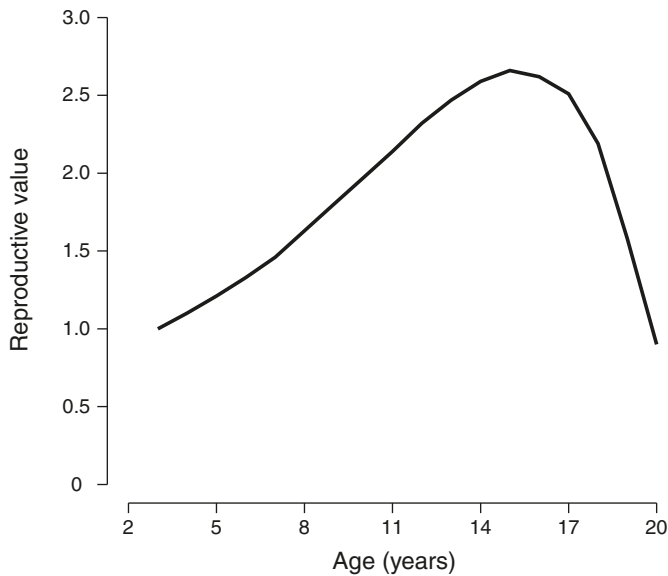
The age-specific reproductive values estimated here underscore the importance to recovery of keeping all human-induced sources of mortality as low as possible to maximize the probability that cod will live to, and reproduce at, these older ages. It is important to note, however, that while such a conclusion may be valid for a population that is at depleted levels (relative to its carrying capacity), the reproductive value of older individuals (relative to younger individuals) can be expected to decline as the population increases in abundance and the strength of density-dependence on survival and fecundity increases.

Do the population dynamics of decline match the population dynamics of recovery?

As a first approximation, it is generally assumed that the rate of recovery of a population can be predicted by its dynamical behaviour during decline. For example, in fisheries science, the stock–recruitment (S–R) relationship of a population in decline is thought to closely approximate the S–R relationship of the same population during recovery (Fig. 8). It is this assumption that underlies the tenet that overfished populations will increase following a significant decrease in fishing mortality, independent of the magnitude of population reduction (Hutchings and Reynolds 2004).

It is also the presumed concordance between the population dynamics of decline and recovery that have underpinned major analyses of Allee effects in marine fishes (e.g., Myers et al. 1995). That is, the slope of a S–R curve, which provides a good approximation (Myers and Mertz 1997; Myers et al. 1997b) of per capita population growth rate, r , is assumed to be highest at the origin (at the smallest of population sizes). Indeed, notwithstanding potential issues pertaining to low statistical power (because of few data near the origin of most S–R relationships), meta-analyses have tended to support the hypothesis that Allee effects are generally not evident in marine fishes (Myers et al. 1995; Liermann and Hilborn 1997; but see Gascoigne and Lipcius 2004). Counter to this conclusion is the observation that increases in natural mortality (M) are not uncommon among depleted populations, e.g., Atlantic cod (Shelton and Healey 1999; Swain 2011), winter skate (*Leucoraja ocellata* (Mitchill, 1815)) (DFO 2005b). In cod, increases in M have been variously attributed to: increased predation (Swain 2011); in-

Fig. 7. Reproductive value of northern Atlantic cod (*Gadus morhua*), based on life-table information available from Hutchings (1999, 2005). Note that the reproductive value between 10 and 15 years is 2.5–3 times higher than that between 3 and 5 years (the data are scaled so that the reproductive value at age 3 is equal to 1).

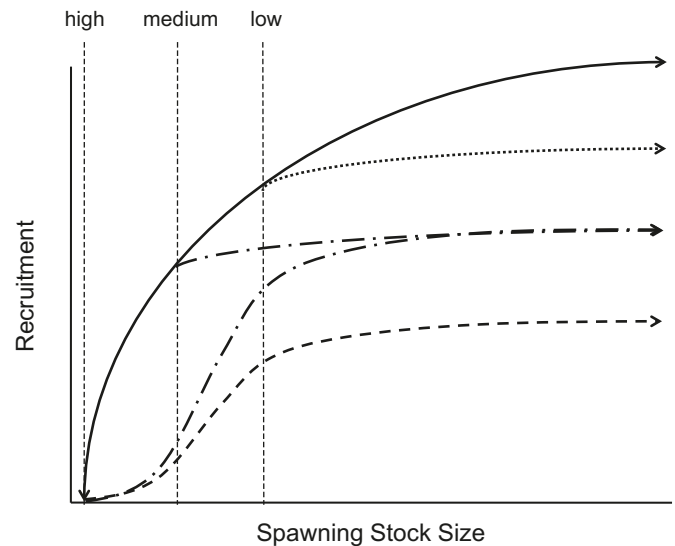


increased competition (Swain and Sinclair 2000); changes in life-history traits (Hutchings 2005; Swain et al. 2007; Swain 2011); and climate-induced variability in recruitment and individual growth (Lilly et al. 2008).

Thus, for some depleted marine fishes, there appears to be good evidence of Allee effects. One interesting question is whether these reductions in r represent an inherent dynamical component of the population in question (a demographic Allee effect sensu Courchamp et al. 2008) or whether they are a consequence of factors such as a truncated age or size distribution or changes in the abundance of interacting species to which an increasingly depleted population becomes increasingly vulnerable (both of which might be considered forms of an emergent Allee effect sensu Courchamp et al. 2008). One example of such an emergent Allee effect would be reductions in r of a depleted population resulting from increases in predator abundance to which the prey's r would not otherwise have been affected if the predator abundance had not increased.

There may be merit in undertaking comparative meta-analyses of S–R relationships to determine whether (i) their dynamics during decline differ from those experienced during recovery and (ii) whether dynamical changes during recovery depend on the magnitude of population depletion. In this regard, one might consider the hypothetical Beverton–Holt S–R curves presented in Fig. 8 that depict potential trajectories of population recovery following three arbitrarily defined levels of decline. Following low, medium, or high reductions in abundance, populations may recover (in a S–R sense) following the same trajectory as that evident during decline. Alternatively, perhaps because of changes in the abundance of other species in the ecosystem, populations may experience slower rates of recovery (reductions in r) than those predicted by the S–R function during the deple-

Fig. 8. Hypothetical trajectories of stock–recruitment (S–R) relationships during population decline and population recovery. The uppermost S–R function (solid arrows) represents one that is the same during recovery as it was during decline. The dotted and dot-dashed S–R functions represent hypothetical S–R relationships during recovery following low and medium depletions, respectively. The depletion is set by the SSB level and the recovery trajectories differ depending upon how highly depleted the stock is. Note that although the slopes at the origin (r_{\max}) are the same for the low- and medium-depletion scenarios, the rates of recovery are reduced (relative to those forecasted from the S–R curve experienced during the depletion phase) because of reductions in carrying capacity. One of the dot-dashed S–R recovery curves for the medium-depletion scenario represents the presence of an emergent Allee effect (e.g., the population dynamics that might result from increased predator abundance). For the high-depletion scenario, both the carrying capacity and r_{\max} have been reduced, the latter to a sufficient extent that the dashed S–R function expresses an demographic Allee effect.



tion phase because of reductions in carrying capacity (reflected by changes in the asymptote of the S–R function for low and medium reductions in abundance). Greater reductions in recovery rate, relative to those forecasted by S–R functions realised during the depletion phase, might be realised by emergent Allee effects (the lower of the two dot-dashed S–R curves in Fig. 8), such as changes in predator–prey interactions or by the loss of individuals that had been present at higher levels of SSB (e.g., larger, older individuals). Reduced rate of recovery relative to that predicted by an S–R function during decline might also be attributable to inherent, demographic Allee effects (the dashed S–R curve associated with the high-depletion scenario).

Changes to S–R relationships during recovery, such as those hypothesized here, will have significant consequences for agencies that incorporate target and limit reference points in fishery management plans (e.g., Chen et al. 2002; DFO 2011b). All else being equal, reductions in r_{\max} and carrying capacity, for example, will reduce the fishing mortality rates and stock biomass levels at which maximum sustainable yield is attained, i.e., F_{msy} and B_{msy} , respectively.

Quantitatively explicit management plans and recovery strategies

Target and limit reference points

One of the greatest risks to the recovery of a depleted fish population is a premature increase in catch quotas (and usually fishing mortality) in response to nascent signs of population increase. These positive signals are often a consequence of strong recruitment, i.e., better-than-average survival of young, pre-reproductive individuals in one or more year classes, or cohorts. Northern cod provide one such example (DFO 2010a) for which recent increases in SSB have been attributed in part to the comparatively strong 1999–2002 year classes. However, because of the comparative weakness of the 2003–2004 year classes (followed by cohorts of average (1993–2007) strength), it has been predicted that, even in the absence of fishing, the recent rate of SSB increase for Northern cod is unlikely to be sustained (DFO 2010a). Thus, the best insurance for some recovery of northern cod is to continue to limit fishing mortality and to not increase catch quotas.

But, in order for such catch restrictions to be deemed acceptable, all those with a vested interest in the sustainability of fishes and fisheries need to be confident that there exists a long-term plan for recovery. It seems self-evident that a fisheries management strategy should include a plan for how to manipulate harvest levels in such a way as to maximize the probability that a target level of abundance can be achieved in as expedient a time as would be biologically feasible (possibly subject to longer times as a result of social and economic considerations). Such a plan would articulate four key elements: (1) a science-determined (as opposed to science-based) recovery target for SSB; (2) a timeline to achieve that target; (3) harvest control rules to govern changes in fishing mortality with changes in SSB; and (4) a science-determined limit reference point for SSB below which directed fishing mortality would be reduced to nil (or very close to nil) and all bycatch mortality would be held at a minimum.

Canada is a signatory to a variety of international agreements pertaining directly or indirectly to the conservation of marine biodiversity, one of which is the United Nations *Agreement on Straddling and Highly Migratory Fish Stocks* (1995), which came into force in 2001. As a signatory, Canada committed itself to adopting the precautionary approach (PA) in managing commercially exploited fishes whose distribution either straddles, or is encompassed by, Canada's 200 nautical mile Exclusive Economic Zone. A variety of articles would appear to attest to this commitment. For example, the preamble to Canada's *Oceans Act* (1996) stipulates that "Canada promotes the wide application of the precautionary approach to the conservation, management and exploitation of marine resources". The Government of Canada's Privy Council Office states explicitly that "The application of...the precautionary approach recognizes that the absence of full scientific certainty shall not be used as a reason for postponing decisions where there is a risk of serious or irreversible harm" (Privy Council Office 2003). However, as comprehensively articulated elsewhere (DFO 2007; Shelton and Sinclair 2008), a defensible argument can be made that although Canada has developed sound, conservation-

based marine fisheries policy in recent years, it has put very little of this policy into practice.

The United Nations Fish Stocks Agreement made explicit the recommendations that signatories determine, on the basis of the best scientific information available, stock-specific target and limit reference points (TRPs and LRPs, respectively) and the actions to be taken if the reference points are exceeded. The United Nations's Food and Agriculture Organization (FAO) guidelines for implementing the Fish Stocks Agreement (FAO 1995), for example, notes that when a LRP is being approached that measures be taken to ensure that the LRP is not exceeded. In effect, the Fish Stocks Agreement stipulates that reference points for fishing mortality (F) and stock biomass (B) be agreed upon to (i) define overfishing (using LRPs), (ii) guide recovery plans (using TRPs), and (iii) develop harvest control rules, using both LRPs and TRPs.

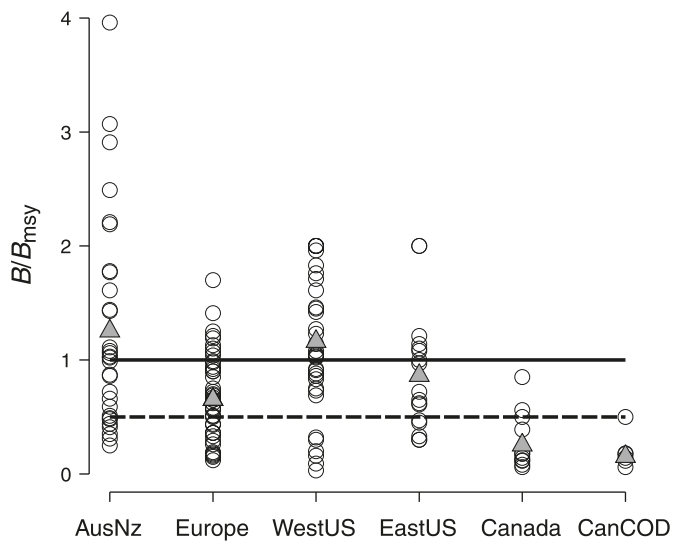
Status of marine fish stocks in relation to B_{msy}

In contrast to the United States, Australia, New Zealand, and the European Union, Canada has not explicitly or formally adopted reference points in the management of its marine fisheries. One consequence of this lack of initiative is that, among industrialized fishing nations, the status of Canada's marine fish stocks is among the worst in the world. Using the stock biomass at which the maximum sustainable yield is estimated to be obtained as a TRP (estimates of B_{MSY} were obtained from stock assessments or surplus production models, as reported by Worm et al. 2009 and Hutchings et al. 2010), the current biomass estimates for Canadian marine fishes are lower than those of other key industrialized fishing nations (Fig. 9).

Although Canadian government fisheries stock assessment scientists have (for several years) been evaluating various methodologies for identifying reference points (Shelton and Rice 2002; DFO 2007), and have previously identified LRPs for Canadian cod (Shelton and Sinclair 2008; DFO 2011b), DFO management has yet to accept these science-determined reference points, to incorporate them in fishery management plans, or to use them as a primary basis for developing harvest control rules. Despite this lack of progress in policy implementation, scientific efforts to estimate reference points for Canadian cod continue (DFO 2011b). One outcome of the most recent discussions is a proposed LRP for northern cod articulated in terms of a fisheries-independent, survey-based catch rate for fish in spawning condition, i.e., a survey SSB catch-rate threshold, of 55 kg/tow (a suggestion not dissimilar to one proffered by Hutchings (1996) as a means of monitoring recovery of the spatial density structure of Northern cod). These recent analyses also indicated that, irrespective of the analytical approach adopted, the current population size of northern cod appears to be at approximately 10% of its LRP (DFO 2011b).

In addition to abundance-based recovery targets, a persuasive argument could also be advanced that recovery objectives should include target distributions of body size and (or) age. Although uncommon, there are precedents for establishing such recovery targets for age distribution, e.g., northeast United States summer flounder (*Paralichthys dentatus* (L., 1766)) (NFSC 2002).

Fig. 9. Current biomass (B) relative to the biomass at which maximum sustainable yield is predicted to be obtained (B_{msy}) for marine fishes managed by fisheries management agencies in Australia and New Zealand (AusNZ; $n = 30$), European Union (Europe; $n = 45$), western United States (WestUS; $n = 37$), eastern United States (EastUS; $n = 17$), Canada ($n = 12$, including stocks of Atlantic cod, *Gadus morhua*), and Canadian stocks of Atlantic cod (CanCOD; $n = 7$). Grey triangles represent the mean value of B/B_{msy} for each region; open circles represent B/B_{msy} for individual stocks. Estimates of B/B_{msy} were obtained from Worm et al. (2009) and Hutchings et al. (2010). The solid and dashed lines identify $B/B_{msy} = 1$ and $B/B_{msy} = 0.5$, respectively, target and limit reference points formally used by the United States, Australia, and New Zealand in their fisheries management plans.



Prescriptive vs. discretionary legislative tools for recovery

As of 2009, all of Canada's cod stocks were either at (St. Pierre Bank) or below the LRPs identified by DFO stock assessment scientists (Figs. 4, 5). Should the federal government accept COSEWIC's 2010 advice to list cod as Endangered under SARA, the ability to directly fish cod would be restricted, although not necessarily prohibited. A directed harvest may be permissible, and included in a recovery strategy, if the Minister of Environment (and presumably the Minister of Fisheries and Oceans) were of the opinion that such harvests would jeopardize neither the survival nor the recovery of the species (SARA, section 73; Vanderzwaag and Hutchings 2005). Recovery strategies developed under the auspices of SARA would require "a statement of the population...objectives that will assist the recovery and survival of the species" (SARA, section 41(1d)). Such recovery objectives would advisedly require the articulation of limit and target reference points for each endangered cod population. However, to date, the federal government has yet to afford Endangered and Threatened marine fishes of commercial interest the recovery and rebuilding frameworks articulated by SARA (Moors et al. 2007; Templeman 2010), arguing in effect that the *Fisheries Act* provides all the necessary legislative tools for recovering depleted marine fishes at heightened risk of extinction.

In the United States, explicit recognition of overfishing and the development of fishery management or rebuilding plans

are undertaken under the auspices of the *Magnuson–Stevens Fishery Conservation and Management Act* (<http://www.nmfs.noaa.gov/sfa/magact/>; accessed 30 March 2011). Amendments in 1996 stipulated very clearly that any management plan prepared by the US Secretary of Commerce (analogous to the Canadian Minister of Fisheries and Oceans) shall contain measures necessary to prevent or end overfishing and to rebuild overfished stocks. This US act is an example of prescriptive, rather than discretionary, legislation insofar as it specifies actions that the Secretary of Commerce shall, or must, take if certain circumstances arise (in this case, if overfishing occurs).

Sections 303 and 304 of the *Magnuson–Stevens Act* are very clear in this regard. A management plan shall specify objective and measurable criteria, i.e., reference points, for determining when a fishery has been overfished. Within 2 years of receiving advice that a fishery has been overfished, the Secretary must establish a plan for rebuilding the overfished stocks such that rebuilding take place over a 10-year period. Although the 10-year time frame may not always be attainable, the key element to the legislation is that it requires that a rebuilding plan be put in place and that limit reference points and rebuilding targets be fundamental components of such plans.

Given that it was under the auspices of Canada's *Fisheries Act* that the historically unprecedented depletions of Atlantic cod (and other marine fishes) took place, a logical argument could be made that it represents a suboptimal legislative tool for fish population recovery and fishery rebuilding purposes. To explore this hypothesis, we searched for various keyword combinations that might reflect the degree to which various pieces of legislation are concerned with recovery or rebuilding. The Acts considered were the *Fisheries Act* (1985), *Oceans Act* (1996), and SARA (2003) in Canada, and *Magnuson–Stevens Fishery Conservation and Management Act* (1996, 2007) in the United States. In the American legislation (408 sections in the Act), the words "recovery", "rebuild", "overfishing", and "target" appear 12, 27, 45, and 22 times, respectively. In the *Fisheries Act* (88 sections), the only one of the four words that appears is "recovery", and it is there twice for the recovery of legal costs rather than the recovery of a fish stock. The *Oceans Act* (52 sections) makes no mention of any of the four words, while SARA (133 sections) mentions "recovery" 83 times.

The Minister of Fisheries and Oceans exercises extraordinary discretionary power (Supreme Court of Canada 1997; Vanderzwaag and Hutchings 2005) and neither the *Fisheries Act* nor the *Oceans Act* can be described as prescriptive pieces of legislation. One empirical example in support of this assertion is provided by a keyword search that compares the number of times that prescriptive action ("minister must" and "minister shall") and discretionary action ("minister may") appear in each of the four pieces of legislation referred to earlier. In the US Act (where "secretary" is synonymous with "minister"), there are 195 instances of "minister shall" and 2 instances of "minister must". However, in the *Fisheries Act*, "minister shall" appears only 3 times (these are related to the furnishing of fisheries inspectors with certificates; an annual report to parliament; and appeals by individuals charged under the Act following property forfeitures), and the words "minister must" do not appear at all. On the other

hand, SARA is highly prescriptive (“minister must” and “minister shall” appearing 53 and 3 times, respectively) with an emphasis on the actions the minister must undertake when specific circumstances arise.

Given the current status of Canada’s marine fish stocks (Fig. 9), and the government’s reluctance to subject marine fishes to the recovery and rebuilding frameworks articulated by SARA, an argument can be made that there is a need for new legislation in Canada, the primary purposes of which would be to prevent overfishing and to rebuild depleted fish stocks. A new law could, among other things, reduce the extremely broad discretionary powers of the Crown from a fisheries perspective (Supreme Court of Canada 1997; Vanderzwaag and Hutchings 2005) and formalize the explicit use of limit and target reference points in fisheries conservation and management. Such legislation would also allow Canada to fulfill key obligations under the various international agreements to which Canada is a signatory. A third objective of such legislation would be to provide a means of formally addressing the regulatory conflict that currently exists within the DFO, insofar as the department has a dual role: promotion of industry and economic activity on the one hand, and the conservation of fish and fish habitat on the other (the simultaneous achievement of these two goals within a single piece of legislation has generally proven ineffective in the Canadian context). Finally, new legislation of the type envisaged here would introduce considerably greater levels of accountability and transparency in efforts to recover depleted marine fishes.

Catalyzing change

The imposition of directed fishing moratoria has often proven insufficient for achieving recovery objectives. Other pressures, such as habitat loss, bycatch, and illegal fishing activity must also be addressed. Management tools are well understood and have proven their value in many jurisdictions. Although legal accountability and responsibilities are clearly addressed in both national and international law, quantitative and precautionary recovery plans as described above have been slow to be implemented in Canada. So what might it take to catalyze change?

The most positive new force for marine conservation, and cod recovery, is growing consumer demand for sustainably sourced seafood. An increasing number of retailers are meeting this demand by pledging to source only sustainable seafood, and many are dropping depleted stocks from their seafood supply in favour of those that meet criteria for well-managed fisheries. In Canada, for example, Loblaw’s Companies Ltd. has committed to sourcing 100% sustainable seafood by the end of 2013 (<http://www.oceansfortomorrow.ca>; accessed 30 March 2011). This trend has been growing rapidly and now includes WalMart in the United States, Carrefour in France, and Sainsbury’s in the United Kingdom.

The Marine Stewardship Council (MSC) is the largest and most credible fisheries certifier (Accenture AG 2009), notwithstanding some concerns in this regard (Jacquet et al. 2010). Well over 6000 products, representing nearly 100 fisheries, have been certified as sustainable in 68 countries. Growth in certifications has literally been exponential in the last few years and with it comes growing market-based pres-

sure for seafood harvesters to seek certification. MSC certification works by setting standards for sustainable fishing and seafood traceability. In addition to having a management system that is responsive to change (to maintain sustainability), the standards must meet three principles which specify that the fishery: (1) operates so that fishing can continue indefinitely without overexploiting resources; (2) minimizes environmental impact and preserves the productivity of the ecosystem; and (3) meets all legal requirements (<http://www.msc.org>; accessed 30 March 2011).

Economic incentives and preferred market share may directly drive industry-led fishery improvements towards MSC certification. In the case of small-quota fisheries, it is possible that markets for cod caught by low-impact fishing methods, such as pots or hook-and-line, may increase the profitability of niche markets. Larger scale economic benefits should also serve as a driver for change. MacGarvin and Jones (2000) estimated that there is an unrealized \$1 billion of potential earnings from sustainable groundfish fisheries in Atlantic Canada, of which cod would be a major component. To achieve this level of recovery, indirect benefits to cod stocks can be addressed through certification of those fisheries that incidentally catch cod as bycatch. For example, the Grand Bank yellowtail flounder (*Limanda ferruginea* (Storer, 1839)) fishery has recently been certified by MSC as a sustainably managed fishery and one of the conditions of the certification is to reduce cod bycatch in this bottom-trawl fishery (<http://www.msc.org>; accessed 30 March 2011).

MSC certifications have, however, come under intense scrutiny and criticism (e.g., Jacquet et al. 2010), and there is a need for MSC to strengthen and reform its certification protocols to maintain itself as an effective tool for fisheries sustainability. Although it is clear that market forces have significant potential to provide direct incentives to change fishing practices, the recovery of cod will require the implementation of a suite of protection and precautionary measures to restore a healthy marine ecosystem in which the species can thrive. More specifically, for the seafood market forces to drive these changes, two challenges will need to be met in order for cod recovery to be sustainable in the long term: (1) enabling ecological conditions will need to be safeguarded and (2) bridge financing will be required to address current gaps in economic incentives for change.

Enabling conditions for recovery

Enabling conditions in ecology are those that maintain or restore resiliency. Area-based management that includes marine protected areas (MPAs) can provide some level of protection for target and nontarget species and essential habitats. These benefits appear to be robust for overfished species (Roberts et al. 2001; Fisher and Frank 2002) and for the restoration of biodiversity and the ecosystem services that accrue (Worm et al. 2006, 2009).

On a considerably broader scale, climate change impacts on the oceans (e.g., increases in temperature, acidity; IPCC 2007) are expected to have many unpredictable consequences (Brander 2008; Cheung et al. 2009). The priority for fisheries and ocean managers should be to focus on managing uncertainty by creating the greatest possible resilience in natural systems. This must be seen as an essential step if marine

ecosystems are to have any chance of effectively adapting to a range of environmental perturbations.

Globally, there is a great dependence on the oceans for both food and commerce. In 2004, global capture fisheries production was 95 million tonnes with an estimated first-sale value of US\$84.9 billion (FAO 2009). Currently, up to one billion people depend on seafood as their primary source of protein (World Bank 2008) and 2.6 billion people rely on fish for at least 20% of their animal-derived protein intake (FAO 2009). Given that the global population is expected to grow from 6.7 billion to an estimated 9.0 billion by 2042 (US Census Bureau 2008), the dependency on ocean-sourced seafood, both wild and farmed, is set to increase rapidly. However, as of 2009, 76% of the fish stocks monitored by the United Nations FAO were assessed as being fully exploited, overexploited, depleted, or recovering from depletion (FAO 2009). As a result, the global fishing industry is losing an estimated \$50 billion annually in potential economic benefits, while the foregone wealth that overfishing has compounded over the last three decades is estimated to be \$2 trillion (World Bank 2008).

Although the link between market forces and well-managed oceans is clear and a potentially a powerful driver for meaningful and effective change, it has not been widely recognized and factored into public debate nor been used to broaden, in any explicit way, the definition of sustainability for seafood purchasing decisions. This opportunity should not be lost given that seafood certification represents a necessary but not sufficient condition for seafood sustainability. There should then be a strong motivation for harvesters to participate in integrated management processes and help promote the adoption of resiliency-building tools, such as MPAs.

Banking on cod

The economic advantages of investing in healthy cod fisheries should provide sufficient incentive for Canadian industry and for Canadian society as whole to drive the development of a long-term recovery plan for Atlantic cod. However, the transition to economically healthy fisheries will still have to resolve the questions of who will bear the burden of costs and how the transition to a fully sustainable and healthy fishing industry will be financed. The challenge of bridging the transition gulf can be met by providing appropriate incentives. There is an increasing array of policy incentives (e.g., credits, tax breaks, co-financing, risk sharing) to induce private capital to invest in priorities of shared interest, using instruments such as private loan capital and equity, venture capital, securities, and futures markets (Davies and Rangeley 2010).

One potential way to finance the transition is to enable harvesters, with the necessary political support, to obtain loans secured against the projected value of future fish stocks to finance a transitional fund. One means of managing risk, damping fluctuations, and guaranteeing prices could be through the use of futures markets. There is considerable precedence for this—the future price of virtually every commodity (e.g., grain, crops, oil) has been the subject of contracts that guarantee future prices. In the case of seafood, fishermen could sell forward-contracts of a fraction of their

catch to investors. Schemes such as this reduce the risks to fishermen and promote conservation by having prices set well in advance. If the stock declines, then the incentive to overfish is reduced because the fishermen are only obligated to sell a fraction of the quota and its value does not increase when fish are rare because the price is moderated in advance (Dalton 2005).

The utility of market forces as a driver for recovery of depleted Canadian Atlantic cod is problematic when there is no return on the immediate costs of necessary management measures. When viewed in this way, it could be argued that the business case for investing in cod recovery really rests with the community of stakeholders affected by fishery management decisions. On the other hand, given that Canada's fisheries are a common property resource that belong to all of the people of Canada (Supreme Court of Canada 1997), the argument can be made that the costs of recovery be borne by all Canadians through the federal government, given that it is all Canadians who ultimately bear the stewardship responsibility to conserve and sustain Canada's marine biodiversity and that it is Canadians who will ultimately be the primary beneficiary of such conservation.

Concluding remarks

The collapse of Canadian Atlantic cod, depending on the population in question, represented the cumulative biological effects of overfishing, temporal and spatial changes in fishing effort, increased harvesting efficiency, oceanographic change, unachieved management objectives, uncertainties in estimating stock abundance, overly ambitious economic policy, and greed (Hutchings and Reynolds 2004; Lilly et al. 2008).

Canada's fishes are a common property resource. The "clients" of the DFO comprise the people of Canada, not exclusively those who derive some part of their income from fishing, seafood processing, or retail. It is the Minister of Fisheries and Oceans' duty to manage, conserve, and develop the fisheries on behalf of Canadians in the public interest (Supreme Court of Canada 1997). In effect, the Minister is responsible for spending and investing the marine biological capital held by all Canadians. Therefore, a "budget" for spending this capital, with quantitative objectives or targets (i.e., TRPs and LRPs), is necessary, such as that expected of a financial manager responsible for managing an individual's or a company's monetary capital.

From a biodiversity perspective, the currently poor status of cod and other fishes, the absence of harvest control rules, and the lack of formal acceptance of science-determined reference points reflects a central problem facing fish and fisheries in Canada: there are negligible political costs associated with government decisions that threaten the health of our oceans.

If cod is to recover, robust management measures must be introduced that adequately and responsibly account for variable population responses to collapse. It is essential to temper harvesting at the first sign of recovery in favour of the establishment of, and adherence to, longer term recovery targets. The transitional recovery period, in whatever form that takes, must also be adequately funded to run its full course so as to avoid pressures to reopen fisheries prematurely. There are unrealized economic benefits that could accrue from healthy

cod fisheries, combined with the associated advantages of reducing economic uncertainty. Economic costs associated with foregoing catches in the short term can be mitigated by longer term financial incentives to focus business and political commitments towards the renewal of cod fisheries and the establishment of a stronger and more profitable seafood industry.

Acknowledgements

We are grateful to Brock Fenton and Sherman Boates for the invitation to write the manuscript. John Bratley, C oil n Minto, and two anonymous reviewers provided very helpful comments on earlier versions of the manuscript. J.A.H. acknowledges those with whom he has undertaken research on Atlantic cod since the early 1990s, notably Ransom Myers and Nick Barrowman. R.W.R. thanks his collaborator in the "Banking on Cod" project, Robin Davies, with whom many of the ideas on conservation financing were developed, as well as the many colleagues associated with WWF's Smart Fishing Initiative for valuable comments and suggestions. We also acknowledge with thanks the dedication of DFO's fisheries stock assessment scientists and the often unheralded excellence of their work on Atlantic cod.

References

- Accenture AG. 2009. Assessment study of on-pack, wild-capture seafood sustainability certification programmes and seafood ecolabels. WWF International, Gland, Switzerland, and Accenture AG, Zurich, Switzerland. Available from http://assets.panda.org/downloads/full_report_wwf_ecolabel_study_lowres.pdf [accessed 8 January 2011].
- Baird, J.W., Bishop, C.A., and Murphy, E.F. 1991. An assessment of the cod stock in NAFO divisions 2J3KL. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Res. Doc. 1991/053.
- Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology, **85**(5): 1258–1264. doi:10.1890/03-0706.
- Beverton, R.J.H., Hysten, A., and Ostvedt, O.J. 1994. Growth, maturation, and longevity of maturation cohorts of northeast Arctic cod. ICES Mar. Sci. Symp. **198**: 482–501.
- Brander, K. 2008. Tackling the old familiar problems of pollution, habitat alteration and over-fishing will help with adapting to climate change. Mar. Pollut. Bull. **56**(12): 1957–1958. doi:10.1016/j.marpolbul.2008.08.024. PMID:18922548.
- Bratley, J., Cadigan, N.G., Healey, B.P., Murphy, E.F., Morgan, M.J., Maddock Parsons, D., Power, D., Dwyer, K., and Mah e, J.-C. 2008. Assessment of the cod stock (*Gadus morhua*) in NAFO Subdivision 3Ps (November 2007). Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Res. Doc. 2008/029.
- Bratley, J., Cadigan, N.G., Dwyer, K., Healey, B.P., Morgan, M.J., Murphy, E.F., Maddock Parsons, D., and Power, D. 2009. Assessment of the cod stock (*Gadus morhua*) in NAFO Divisions 2J+3KL in 2009. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Res. Doc. 2009/061.
- Chen, D.G., Irvine, J.R., and Cass, A.J. 2002. Incorporating Allee effects in fish stock-recruitment models and applications for determining reference points. Can. J. Fish. Aquat. Sci. **59**(2): 242–249. doi:10.1139/f02-005.
- Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., and Pauly, D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish. **10**(3): 235–251 doi:10.1111/j.1467-2979.2008.00315.x.
- Childs, D.Z., Metcalf, C.J.E., and Rees, M. 2010. Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. Proc. R. Soc. Lond. B Biol. Sci. **277**(1697): 3055–3064. doi:10.1098/rspb.2010.0707. PMID:20573624.
- Cole, L.C. 1954. The population consequences of life history phenomena. Q. Rev. Biol. **29**(2): 103–137. doi:10.1086/400074. PMID:13177850.
- COSEWIC. 2010. Update COSEWIC status report on Atlantic cod, *Gadus morhua*. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ont.
- Courchamp, F., Berec, L., and Gascoigne, J. 2008. Allee effects in ecology and conservation. Oxford University Press, Oxford.
- Dalton, R. 2005. Fishy futures. Nature (London), **437**(7058): 473–474. doi:10.1038/437473a. PMID:16177759.
- Davies, R.W.D., and Rangeley, R.W.R. 2010. Banking on cod: exploring economic incentives for recovering Grand Banks and North Sea cod fisheries. Mar. Policy **34**(1): 92–98. doi:10.1016/j.marpol.2009.04.019.
- deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. **50**(12): 2729–2741. doi:10.1139/f93-298.
- DFO. 2003. Northern (2J+3KL) cod. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Stock Status Rep. 2003/018.
- DFO. 2005a. Stock assessment report on Northern (2J+3KL) cod. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Science Advisory Rep. 2005/024.
- DFO. 2005b. Recovery potential assessment for winter skate on the Eastern Scotian Shelf (NAFO division 4VW). Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Science Advisory Rep. 2005/062.
- DFO. 2007. Assessing marine fish species: relating approaches based on reference points with approaches based on rate-of-extinction. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Proceedings Ser. 2007/024.
- DFO. 2009a. Stock assessment of subdivision 3Ps cod. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Science Advisory Rep. 2009/008.
- DFO. 2009b. Assessment of cod in the Southern Gulf of St. Lawrence. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Science Advisory Rep. 2009/007.
- DFO. 2009c. Cod on the Southern Scotian Shelf and in the Bay of Fundy (Div. 4X/5Y). Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Science Advisory Rep. 2009/015.
- DFO. 2010a. Stock assessment of Northern (2J3KL) cod in 2010. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Science Advisory Rep. 2010/019.
- DFO. 2010b. 2010 Canadian marine ecosystem status and trends report. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Science Advisory Rep. 2010/030.
- DFO. 2010c. Assessment of the cod stock in the Northern Gulf of St. Lawrence (3Pn,4RS) in 2009. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Science Advisory Rep. 2010/011.
- DFO. 2011a. Impacts of grey seals on fish populations in eastern Canada. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Science Advisory Rep. 2010/071.
- DFO. 2011b. Proceedings of the Newfoundland and Labrador regional Atlantic cod framework meeting: reference points and projection methods for Newfoundland cod stocks; November 22–

- 26, 2010. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Proceedings Ser. 2010/053.
- Drinkwater, K.F. 2002. A review of the role of climate variability in the decline of northern cod. *Am. Fish. Soc. Symp.* **32**: 113–130.
- Fanning, L.P., Mohn, R.K., and MacEachern, W.J. 2003. Assessment of 4VsW cod to 2002. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Res. Doc. 2003/027.
- FAO. 1995. Code of conduct for responsible fisheries. Food and Agriculture Organization (FAO) of the United Nations, Rome.
- FAO. 2009. The state of world fisheries and aquaculture 2008. Food and Agriculture Organization (FAO) of the United Nations, Rome.
- Fisher, R.A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.
- Fisher, J.A.D., and Frank, K.T. 2002. Changes in finfish community structure associated with an offshore fishery closed area on the Scotian Shelf. *Mar. Ecol. Prog. Ser.* **240**: 249–265. doi:10.3354/meps240249.
- Fudge, S.B., and Rose, G.A. 2008. Life history co-variation in a fishery depleted Atlantic cod stock. *Fish. Res.* **92**(1): 107–113. doi:10.1016/j.fishres.2008.02.005.
- Gascoigne, J., and Lipcius, R.N. 2004. Allee effects in marine systems. *Mar. Ecol. Prog. Ser.* **269**: 49–59. doi:10.3354/meps269049.
- Hardie, D.C., and Hutchings, J.A. 2011. The ecology of Atlantic cod (*Gadus morhua*) in Canadian Arctic lakes. *Arctic*. In press.
- Hilborn, R., and Litzinger, E. 2009. Causes of decline and potential for recovery of Atlantic cod populations. *Open Fish Sci. J.* **2**(1): 32–38. doi:10.2174/1874401X00902010032.
- Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Can. J. Fish. Aquat. Sci.* **53**(5): 943–962. doi:10.1139/cjfas-53-5-943.
- Hutchings, J.A. 1999. The influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. *Can. J. Fish. Aquat. Sci.* **56**(9): 1612–1623. doi:10.1139/cjfas-56-9-1612.
- Hutchings, J.A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **62**(4): 824–832. doi:10.1139/f05-081.
- Hutchings, J.A., and Myers, R.A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **50**(11): 2468–2474. doi:10.1139/f93-271.
- Hutchings, J.A., and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.* **51**(9): 2126–2146. doi:10.1139/f94-214.
- Hutchings, J.A., and Myers, R.A. 1995. The biological collapse of Atlantic cod off Newfoundland and Labrador: an exploration of historical changes in exploitation, harvesting technology, and management. *In* The North Atlantic fishery: strengths, weaknesses, and challenges. *Edited by* R. Arnason and L.F. Felt. Institute of Island Studies, University of Prince Edward Island, Charlottetown. pp. 37–93.
- Hutchings, J.A., and Reynolds, J.D. 2004. Marine fish population collapses: consequences for recovery and extinction risk. *Bioscience*, **54**(4): 297–309. doi:10.1641/0006-3568(2004)054[0297:MFPCCF]2.0.CO;2.
- Hutchings, J.A., Minto, C., Ricard, D., Baum, J.K., and Jensen, O.P. 2010. Trends in the abundance of marine fishes. *Can. J. Fish. Aquat. Sci.* **67**(8): 1205–1210. doi:10.1139/F10-081.
- IPCC. 2007. Fourth assessment report: climate change 2007. International Panel on Climate Change (IPCC), Geneva, Switzerland.
- Jacquet, J., Pauly, D., Ainley, D., Holt, S., Dayton, P., and Jackson, J. 2010. Seafood stewardship in crisis. *Nature (London)*, **467**(7311): 28–29. doi:10.1038/467028a. PMID:20811437.
- Jørgensen, C., and Fiksen, Ø. 2010. Modelling fishing-induced adaptations and consequences for natural mortality. *Can. J. Fish. Aquat. Sci.* **67**(7): 1086–1097. doi:10.1139/F10-049.
- Kjesbu, O.S. 1989. The spawning activity of cod, *Gadus morhua* L. *J. Fish. Biol.* **34**(2): 195–206. doi:10.1111/j.1095-8649.1989.tb03302.x.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* **142**(6): 911–927. doi:10.1086/285580.
- Liermann, M., and Hilborn, R. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.* **54**(9): 1976–1984. doi:10.1139/cjfas-54-9-1976.
- Lilly, G.R. 1997. Size and condition of cod in Divisions 2J+3KL during 1978–1996. NAFO SCR Doc. 97/62, Ser. No. N2869.
- Lilly, G.R., Wieland, K., Rothschild, B.J., Sundy, S., Drinkwater, K. F., Brander, K., Ottersen, G., Carscadden, J.E., Stenson, G.B., Chouinard, G.A., Swain, D.P., Daan, N., Enberg, K., Hammill, M. O., Rosing-Asvid, A., Svedäng, H., and Vásquez, A. 2008. Decline and recovery of Atlantic cod (*Gadus morhua*) stocks throughout the North Atlantic. *In* Resiliency of gadid stocks to fishing and climate change. *Edited by* G.H. Kruse, K. Drinkwater, J.N. Ianelli, J.S. Link, D.L. Stram, V. Weststad, and D. Woodby. Alaska Sea Grant College Program, Fairbanks. pp. 39–66.
- MacGarvin, M., and Jones, S. 2000. Choose or lose: a recovery plan for fish stocks and the UK fishing industry. Available from <http://www.wwf.org.uk/filelibrary/pdf/chooseorlose.pdf> [accessed 13 January 2011].
- Mooers, A.Ø., Prugh, L.R., Festa-Bianchet, M., and Hutchings, J.A. 2007. Biases in legal listing under Canadian endangered species legislation. *Conserv. Biol.* **21**(3): 572–575. doi:10.1111/j.1523-1739.2007.00689.x.
- Myers, R.A., and Mertz, G. 1997. Maximum population growth rates and recovery times for Atlantic cod (*Gadus morhua*). *Fish. Bull. (Wash., D.C.)*, **95**: 762–772.
- Myers, R.A., Barrowman, N.J., Hutchings, J.A., and Rosenberg, A.A. 1995. Population dynamics of exploited fish stocks at low population levels. *Science (Washington, D.C.)*, **269**(5227): 1106–1108. doi:10.1126/science.269.5227.1106. PMID:17755535.
- Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1997a. Why do fish stocks collapse? The example of cod, *Gadus morhua*, in Atlantic Canada. *Ecol. Appl.* **7**(1): 91–106. doi:10.1890/1051-0761(1997)007[0091:WDFSC]2.0.CO;2.
- Myers, R.A., Mertz, G., and Fowlow, P.S. 1997b. Maximum population growth rates and recovery times for Atlantic cod (*Gadus morhua*). *Fish. Bull. (Wash., D.C.)*, **95**: 762–772.
- NFSC. 2002. Report of the 35th Northeast Regional Stock Assessment Workshop (35th SAW): public review workshop. Northeast Fisheries Science Center (NFSC) Ref. Doc. 02-13. NFSC, Woods Hole, Mass.
- Olsen, E.B., Lilly, G.R., Heino, M., Morgan, M.J., Brattey, J., and Dieckmann, U. 2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **62**(4): 811–823. doi:10.1139/f05-065.
- Power, D., Morgan, J., Murphy, E.F., Brattey, J., and Healey, B. 2010. An assessment of the cod stock in NAFO divisions 3NO. NAFO SCR Doc. No. 10/42.
- Privy Council Office. 2003. A framework for the application of precaution in science-based decision making about risk. Privy Council Office, Government of Canada, Ottawa, Ont.
- Roberts, C.M., Bohnsack, J.A., Gell, F.R., Hawkins, J.P., and

- Goodridge, R. 2001. Effects of marine reserves on adjacent fisheries. *Science* (Washington, D.C.), **294**(5548): 1920–1923. doi:10.1126/science.294.5548.1920. PMID:11729316.
- Roff, D.A. 1981. Reproductive uncertainty and the evolution of iteroparity: why don't flatfishes put all their eggs in one basket? *Can. J. Fish. Aquat. Sci.* **38**(8): 968–977. doi:10.1139/f81-130.
- Roff, D.A. 1984. The evolution of life-history parameters in teleosts. *Can. J. Fish. Aquat. Sci.* **41**(6): 989–1000. doi:10.1139/f84-114.
- Roff, D.A. 2002. Life history evolution. Sinauer Associates Inc., Sunderland, Mass.
- Rose, G.A. 2004. Reconstructing overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. *Can. J. Fish. Aquat. Sci.* **61**(9): 1553–1557. doi:10.1139/f04-173.
- Rose, G.A. 2007. Cod: the ecological history of the North Atlantic fisheries. Breakwater, St. John's, N.L.
- Rowe, S., Hutchings, J.A., Skjæraasen, J.E., and Bezanson, L. 2008. Morphological and behavioural correlates of reproductive success in Atlantic cod, *Gadus morhua*. *Mar. Ecol. Prog. Ser.* **354**: 257–265. doi:10.3354/meps07175.
- Shelton, P.A., and Healey, B.P. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern Atlantic cod (*Gadus morhua*) stock? *Can. J. Fish. Aquat. Sci.* **56**(9): 1521–1524. doi:10.1139/cjfas-56-9-1521.
- Shelton, P.A., and Rice, J.C. 2002. Limits to overfishing: reference points in the context of the Canadian perspective on the precautionary approach. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Res. Doc. 2002/054.
- Shelton, P.A., and Sinclair, A.F. 2008. It's time to sharpen our definition of sustainable fisheries management. *Can. J. Fish. Aquat. Sci.* **65**(10): 2305–2314. doi:10.1139/F08-151.
- Supreme Court of Canada. 1997. Comeau's Sea Foods Ltd. v. Canada (Minister of Fisheries and Oceans), [1997] 1 S.C.R. 12. Supreme Court of Canada File No. 24682. Available from <http://scc.lexum.org/en/1997/1997scr1-12/1997scr1-12.html> [accessed 8 January 2011].
- Swain, D.P. 2011. Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). *Evol. Appl.* **4**(1): 18–29. doi:10.1111/j.1752-4571.2010.00128.x.
- Swain, D.P., and Chouinard, G. 2008. Predicted extirpation of the dominant demersal fish in a large marine ecosystem: Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* **65**(11): 2315–2319. doi:10.1139/F08-175.
- Swain, D.P., and Sinclair, A.F. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **57**(7): 1321–1325. doi:10.1139/cjfas-57-7-1321.
- Swain, D.P., Sinclair, A.F., and Hanson, J.M. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proc. R. Soc. Lond. B Biol. Sci.* **274**(1613): 1015–1022. doi:10.1098/rspb.2006.0275. PMID:17264058.
- Templeman, N.D. 2010. Ecosystem status and trends report for the Newfoundland and Labrador Shelf. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Res. Doc. 2010/026.
- Trippel, E.A., Morgan, M.J., Fréchet, A., Rollet, C., Sinclair, A., Annand, C., Beanlands, D., and Brown, L. 1997. Changes in age and length at sexual maturity of Northwest Atlantic cod, haddock and pollock stocks, 1972–1995. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 2157.
- US Census Bureau. 2008. Population Division: international data base (IDB). Available from <http://www.census.gov/ipc/www/idb/worldpopgraph.php> [accessed 13 January 2011].
- Vallin, L., and Nissling, A. 2000. Maternal effects on egg size and egg buoyancy of Baltic cod (*Gadus morhua*): implications for stock structure effects on recruitment. *Fish. Res.* **49**(1): 21–37. doi:10.1016/S0165-7836(00)00194-6.
- Vanderzwaag, D.L., and Hutchings, J.A. 2005. Canada's marine species at risk: science and law at the helm, but a sea of uncertainties. *Ocean Dev. Int. Law*, **36**(3): 219–259. doi:10.1080/00908320591004333.
- Venturelli, P.A., Shuter, B.J., and Murphy, C.A. 2009. Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. *Proc. R. Soc. Lond. B Biol. Sci.* **276**(1658): 919–924. doi:10.1098/rspb.2008.1507. PMID:19033140.
- Williams, G.C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, N.J.
- Worcester, T., Bratley, J., Chouinard, G.A., Clark, D., Clark, K.J., Deault, J., Fowler, M., Fréchet, A., Gauthier, J., Healey, B., Lambert, Y., Maddock Parsons, D., Mohn, R., Morgan, M.J., Murphy, E.F., Power, D., Powles, H., Schwab, P., Swain, D.P., and Treble, M. 2009. Status of Atlantic cod (*Gadus morhua*) in 2008. Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Res. Doc. 2009/027.
- World Bank. 2008. Sunken billions: the economic justification for fisheries reform. Agriculture and Rural Development, The World Bank and FAO.
- Worm, B., and Myers, R.A. 2003. Meta-analysis of cod–shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, **84**(1): 162–173. doi:10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., and Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* (Washington, D.C.), **314**(5800): 787–790. doi:10.1126/science.1132294. PMID:17082450.
- Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., and Zeller, D. 2009. Rebuilding global fisheries. *Science* (Washington, D.C.), **325**(5940): 578–585. doi:10.1126/science.1173146. PMID:19644114.