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Age at Maturity as a Stress Indicator in Fisheries

Biological processes related to reproduction in northwest Atlantic groundfish populations that have undergone declines

Edward A. Trippel

On 2 July 1992 the largest Atlantic cod (*Gadus morhua*) fishery in the northwest Atlantic was closed to commercial fishing by Canada's Minister of Fisheries. For more than 350 years, this fishery provided food and income for the many communities scattered along the east coast of Newfoundland. The Newfoundland fishing industry, based on the annual migration of cod from offshore spawning grounds of the Grand Bank to inshore feeding areas, had been the mainstay of the province's economy (Figure 1).

In the 1950s, additional large winter aggregations of cod were located offshore of Newfoundland in water depths of 100–200 fathoms (Johnstone 1977). This discovery prompted the development of a large-trawler offshore fishery, which included foreign vessels, and annual landings increased through the 1960s. By the mid-1970s stock¹ size had declined, but it subsequently increased after Canada began to exert control over fishing rights within 200 miles of its coastline on 1 January 1977. (Before 1977 Canada's jurisdiction was limited to within 12 miles of shore). Foreign landings declined over time

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Use of age at maturity as an indicator of changes in population size holds promise

within Canada's 200-mile limit. Through the early 1980s, the size of the Grand Bank cod stock improved. Then, from 1989 to 1992, the cod fishery was devastated both in offshore and inshore areas. A record of the decline in stock size of the Grand Bank, Newfoundland, cod as indicated by research-vessel survey data is shown in Figure 2.

Declines, although not as precipitous as for Grand Bank cod, have occurred in other northwest Atlantic cod stocks (Figure 2). In addition to cod, flatfish stock sizes also have declined dramatically in recent years. The reductions in stock sizes have led to the present fishing closures of seven of eight cod stocks in the northwest Atlantic. Many of the more than 40,000 commercial fishermen who had fished for groundfish in the northwest Atlantic during the past five years have been forced to abandon their traditional livelihood. Only the relatively small southern cod stock of the southern Nova Scotian Shelf and Bay of Fundy has a directed fishery

¹Stock (or population) is defined as a group of interbreeding fish that commonly inhabit a defined geographical area.

in 1995 with a quota of 9000 metric tons. For the Georges Bank cod (a transboundary stock between Canada and the United States), a nondirected by-catch quota of 1000 metric tons was set for 1995. Stocks of cod, haddock (*Melanogrammus aeglefinus*), and a variety of flatfish species on the US portion of Georges Bank also have been severely depleted and are now managed by the United States under near-moratoria regulations of record low allowable catches (CUD 1993).

Landings for all cod stocks in Canada in 1987 were 452,000 metric tons, whereas after imposition of a moratorium on Grand Bank cod and closures and reductions in allowable catches for other cod stocks, the total catch declined to 81,000 metric tons in 1993 and further to 22,000 metric tons in 1994. Of the potential causes, overfishing, predation on cod by increasing numbers of seals, cold seawater conditions, reduction in forage fish for cod, and poor production of young cod to replace the declining adult populations are often cited as being principally responsible for the decline in cod stocks of the northwest Atlantic. Before the closures, it was not uncommon in some stocks for cod harvesting rates to exceed a level at which 60% of the older adult biomass was removed annually, as opposed to the 20% rate recommended to sustain such fisheries (Halliday and Pinhorn 1985). The recovery of northwest Atlantic cod stocks is critically dependent on spawning fish.

Low egg production and the loss of large cod from stocks are now common concerns among fishermen and scientists alike. On the Grand Banks, in 1991 there was an abrupt decline of cod in the age range 7–20 years; the numbers dropped to approximately 10% of the long-term average (Baird et al. 1992).

Ron Henneberry, a fifth-generation commercial fisherman of Eastern Passage, Nova Scotia, has observed landings of groundfish in the northwest Atlantic Ocean since boyhood (Figure 3). He says that over the years fish such as cod, haddock, and pollock (*Pollachius virens*) are not only fewer in number but also smaller in size.² The diminution in number of large fish, which normally produce millions of eggs each, has put the burden of future progeny production on small-sized fish and raises concerns whether these young adults are sufficient in their reproductive capacity to return stock sizes to their levels in the mid-1980s and earlier.

This article provides an overview, based on existing knowledge, of the biological processes related to reproduction in stressed populations. A stressed population is defined as one that has undergone a substantial decline in size (Shuter 1990). The information presented in this article is intended to be useful to fishery managers who make decisions regarding resource conservation and rebuilding. The main focus is on groundfish and the present crisis in the northwest Atlantic.

To address the problems of the Atlantic fishery, the Canadian federal government recently formed the Fisheries Resource Conservation Council, which is presently considering options for establishing minimal stock biological reference points that safeguard against stock collapse. The council is also identifying biological criteria or thresholds to be met before closed stocks are reopened.

For each fishery under US federal management, the government requires definitions of overfishing that guard against reducing a popula-



Figure 1. Newfoundland inshore fishermen landing their catches of Atlantic cod in the port of Bonavista in 1950. Fishermen would either fish with hook and line or trap nets, and they would return, with their catches, to shore daily.

tion to a level at which the production of young is seriously impaired. Regulations published in July 1989 require US fisheries management plans to "...specify, to the maximum extent possible, an objective and measurable definition of overfishing for each stock or stock complex covered by that Fisheries Management Plan, and to provide an analysis of how the definition was determined and how it relates to reproductive potential" (Mace and Sissenwine 1993). These plans are developed by US Fishery Management Councils and the National Marine Fisheries Service. For example, in this context, Mace and Sissenwine (1993) have identified reference spawning stock biomass thresholds for 83 marine fish stocks below which the size of a year class produced is less than 50% of the long-term average. Year class size is defined as the number of young fish produced by a population each year, and it varies in response to a number of biological and environmental factors such as egg production, predation, starvation, water temperature, and other elements of hydrography.

Spawning stock biomass is the cumulative weight of all sexually mature fish and is commonly used to represent egg production. The relationship between spawning stock biomass and resultant year class size

can be highly variable in northwest Atlantic cod stocks, though in some stocks (including the Grand Bank cod) a large year class frequently originates from large spawning stock biomass (Maguire and Mace 1993).

A long-lived species such as cod is capable of having approximately 15 year classes coexisting (i.e., ages 1–15 years) in, for example, lightly exploited populations (Scott and Scott 1988). Thus, considering that sexual maturity is typically reached in less than five years, in a lightly exploited cod population an individual may spawn more than five times before dying of natural causes (natural mortality rate assumed of 20% per year). Also, because cod continue to grow after maturity, in each successive breeding year a spawning cod is likely to be larger, although rate of growth declines late in life. Cod can attain body sizes in excess of 1.5 m and 40 kg (Figure 4). High mortality due to fishing dramatically decreases probability of a fish's surviving beyond several years, so it can effectively change a fish population with many year classes into one with only few. For example, due to recent high exploitation rates, a large number of Georges Bank cod are only spawning once in their lives before being caught, and some are harvested in a sexually immature state (Hunt in press, Trippel et al. 1995).

²Ron Henneberry, 1995, personal communication. Commercial fisherman, Eastern Passage, Nova Scotia, Canada.

Atlantic cod

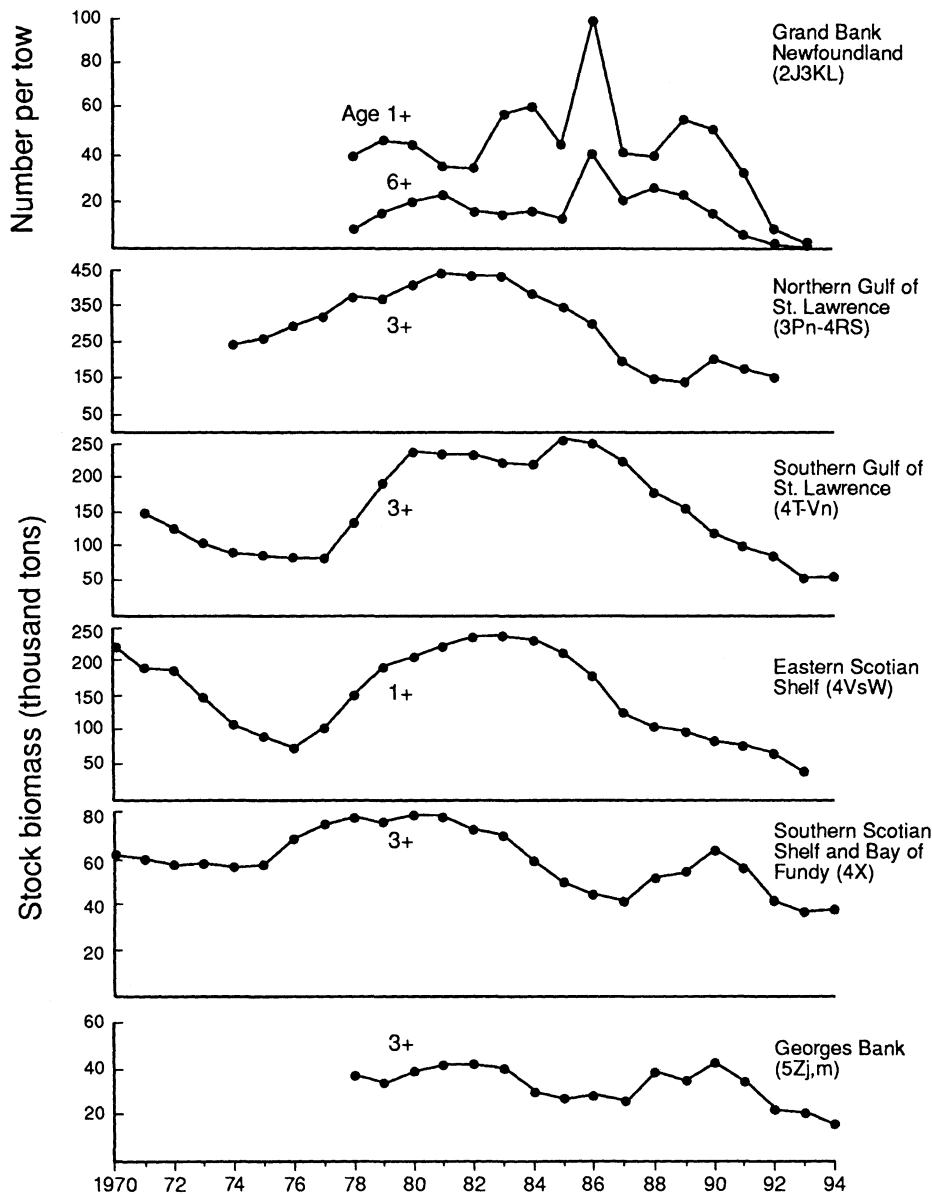


Figure 2. Recent trends in stock sizes of Atlantic cod in the northwest Atlantic. Age-plus groups (e.g., 1+ refers to age one year and older) and the Northwest Atlantic Fisheries Organization (NAFO) unit areas are presented for each stock. Abundance of Grand Bank cod in NAFO Divisions 2J3KL is represented by research survey data, specifically the average number caught during 30-minute tows of an otter trawl, whereas other stocks are represented by estimated population sizes (Sources: Anonymous 1993, 1994, Sinclair 1993). Grand Bank cod stock sizes from 1992–1994 were not available, though historically this stock is the largest of the Canadian cod stocks; between 1962 and 1977 the stock biomass age 7+ declined from 1.5 million to 100,000 metric tons, after which it increased to 500,000 metric tons during the 1980s (Baird et al. 1992).

Sizes of large oceanic fish populations are difficult to estimate accurately because of large uncertainties in a number of the parameters required for fish population mod-

els. Such uncertainties include inaccuracy of landings statistics, assumed estimates of natural mortality, and variability in results of population abundance surveys.

Commercial catch rates are potentially useful to estimate fish abundance. However, cases of misreporting of catches, discarding fish at sea, changing fishing practices, and modifying gear reduce the usefulness of some of these abundance measures. For many fish stocks, reliable estimates of population size do not exist, and scientists and managers are therefore interested in identifying corroborative sources of evidence that can be used to gauge and monitor population size.

Age at first maturity is a candidate indicator of stock size and is simple to measure. Maturity responses such as a lowering in age at maturity may document an important stock response to reductions in population size. Thus, by annually measuring age at maturity, one may indirectly be able to follow trends in population size. Data on sexual maturity have been collected on some fish stocks for nearly a century beginning with two major marine fish populations in the northeast Arctic and North Sea (Jørgensen 1990, Rijnsdorp 1993a). Maturity state is determined by visual inspection of the gonads for evidence of mature eggs or sperm. Age of a sampled individual is evaluated by counting annual rings of microscopic size deposited in calcified structures such as small ear bones called otoliths (Penttila and Dery 1988). Not all individuals within a population reach their first year of reproductive activity at the same age. Typically, it takes one year for an immature cod to fully develop mature sexual organs, and maturation begins at ages one to six years; cod in northerly populations mature later in life than do those in southern waters (Hunt in press, Morgan et al. 1993).

In addition to age at maturity, body length at first maturity varies within and among populations and generally ranges from 30 to 50 cm among northwest Atlantic cod populations (Trippel and Neilson 1992, Trippel et al. 1995). Age and length at maturity are closely related, and although the primary focus of this article is age at maturity, its covariation with length at maturity is discussed.

This article describes the shifts

that have been observed in age at maturity in exploited fish stocks and focuses on the possible consequences that declines in age at maturity have on the reproductive potential of a stock (i.e., egg production, egg size, and seasonal timing of spawning). Although data on age at maturity may be simple to collect, the determination of the reasons for shifts in age at maturity is often difficult. Use of age at maturity as an indicator of changes in population size holds promise, though it requires evaluation from several perspectives.

Early maturity

During the decades of exploitation, changes have occurred in the age at maturity of a number of populations worldwide. Fish are breeding at ages much younger than previously observed (Tables 1–3). The extent of declines in age at maturity varies among studies. Beacham (1983a, b, c) and Hunt (in press) have studied the northwest Atlantic cod stocks. Beacham showed a re-



Figure 3. A side-trawler capturing Atlantic cod off the coast of Nova Scotia on La Have Bank in the early 1950s. One of the two large doors of the otter trawl is seen suspended next to the vessel and is used to spread the net as it is towed along the ocean bottom. Trawlers have remained an important component of the overall fishing fleet in the northwest Atlantic.

Table 1. Changes in age at maturity in exploited Atlantic cod (*Gadus morhua*) populations over various time periods. Maturity trends are shown separately for specific Northwest Atlantic Fisheries Organization Subdivisions (e.g., 4Vn, 4Vs, 4W, and 4X of the Scotian Shelf). Within a population, the transition from 0% (an age at which no fish are mature) to 100% maturity (an age at which all fish are mature) typically spans several years. Age at maturity for a population is analyzed by fitting curves such as the probit or logistic model to estimates of the percentage of fish mature at different ages (e.g., 0%, 25%, 50%, 75%, and 100% for fish sampled of ages two through six years, and in this example age at 50% maturity would be four years; Trippel and Harvey 1991). When fish are sampled from the population some years later, a shift to earlier maturity in the above hypothetical example may be represented by maturity of 0%, 25%, 50%, 75%, and 100% for ages one through five years, where the percentage of mature fish in each age class has increased. Age at 50% (median) maturity in this example declined from four to three years.

Location	Subdivision	Period	Sex	Age at maturity* (year)			Source
				At beginning and end of period	Magnitude of change	Percent change	
Northwest Atlantic Grand Bank	3L	1978–1992	F	6.07–5.08	0.99	-16.3	Morgan et al. 1993
			M	5.10–4.06	1.04	-20.3	
Gulf of St. Lawrence	4T	1959–1979	F	6.08–3.60	2.48	-40.8	Beacham 1983a ¹
			M	4.96–3.58	1.38	-27.8	
Scotian Shelf	4Vn	1959–1979	F	6.34–2.78	3.56	-56.2	Beacham 1983b
			M	5.58–3.08	2.50	-44.8	
	4Vs	F	5.19–2.86	2.33	-44.9		
		M	5.43–2.72	2.71	-49.9		
	4W	F	4.95–2.87	2.08	-42.0		
		M	4.69–2.67	2.02	-43.1		
4X	F	3.72–2.88	0.84	-22.6			
	M	4.76–2.78	1.98	-41.6			
Georges Bank	5Z	1986–1993	F+M	2.30–1.87	0.43	-18.7	Hunt in press
Northeast Arctic		1923–1976	F+M	10.75–7.65	3.10	-28.8	Jørgensen 1990

*Values presented are predominantly median (50%) age at maturity (Trippel and Harvey 1991).

¹Although some values of Beacham's findings are subject to criticism (Halliday 1987), the general trend toward earlier maturity is evident.

Table 2. Changes in age at maturity in exploited haddock (*Melanogrammus aeglefinus*). See Table 1.

Location	Subdivision	Period	Sex	Age at maturity* (year)			Source
				At beginning and end of period	Magnitude of change	Percent change	
Scotian Shelf	4Vn	1959–1979	F	4.40–3.54	0.86	-19.5	Beacham 1983c
			M	3.63–3.24	0.38	-10.5	
	4Vs		F	4.31–2.74	1.57	-36.4	
			M	3.78–2.83	0.95	-25.1	
	4W		F	4.40–3.11	1.29	-29.3	
			M	3.88–2.76	1.12	-28.9	
	4X		F	4.61–3.02	1.59	-34.5	
			M	4.74–2.83	1.91	-40.3	

*Values presented are predominantly median (50%) age at maturity (Trippel and Harvey 1991).

Table 3. Fish other than cod and haddock. See Table 1.

Species	Subdivision	Period	Sex	Age at maturity* (year)			Source
				At beginning and end of period	Magnitude of change	Percent change	
Witch flounder (<i>Glyptocephalus cynoglossus</i>) Grand Bank	2J	1973–1983	F	10.33–7.38	2.95	-28.6	Bowering and Brodie
	3K	1970–1983	F	7.92–7.66	0.26	-3.30	
	3L	1968–1983	F	9.43–7.87	1.56	-16.5	
American plaice (<i>Hippoglossoides platessoides</i>) Grand Bank	3L	1961–1972	F	13.98–10.57	3.41	-24.4	
	3N	1957–1971	F	11.07–8.79	2.28	-20.6	
	3Ps	1973–1988	F	10.63–9.43	1.15	-10.8	
Plaice (<i>Pleuronectes platessa</i>) North Sea		1900–1985	F	6–4	2	-33.3	Rijnsdorp 1993a
			M	5–2	3	-60.0	
Walleye (<i>Stizostedion vitreum</i>) Lake Erie		1927–1966	F	(4–5)–3	1–2	~ -30.0	Spangler et al. 1977
			M	(3–4)–2	1–2	~ -43.8	
Yellow perch (<i>Perca flavescens</i>) Lake Erie			F	3–2	1	-33.3	
Lake whitefish (<i>Coregonus clupeaformis</i>) Lake Michigan		1932–1967	F+M	4.2–2.5	1.7	-40.5	Taylor et al. 1992
Striped bass (<i>Morone saxatilis</i>) Coastal Rhode Island		1941–1987	F	4.6–5.3	0.7	+15.2	Berlinsky et al. 1995

*Values presented are predominately median (50%) age at maturity (Trippel and Harvey 1991).

duction, over a 20-year period, of 2 to 3 years in the median age at sexual maturity in stocks spanning from the Bay of Fundy northwards to the Gulf of Saint Lawrence (in one stock in Northwest Atlantic Fisheries Organization Subdivision 4V the age of maturity decreased from 6.3 to 2.8 years from 1959 to 1979; see Table 1). These declines are substantial and amount to 40%–55% reductions in age at maturity.

Natural variation in age at matu-

rity typically produces less rapid fluctuation. For example, in northeast Arctic cod, age at maturity varied at a rate of 0.1 years per year for 16 years (1930–1946) and remained stable from 1950–1957 (Jørgensen 1990). Minor variations of this magnitude may be considered to reflect stable or equilibrium conditions. Pronounced declines in the age at maturity for northeast Arctic cod occurred between 1959–1969, when decreases were from 10.2 to 7.5 years or approximately 0.3 years per year.

In addition, for flatfish stocks of the Grand Banks, age at maturity also declined as much as 3.4 years (or 25%) over an 11-year period in American plaice (*Hippoglossoides platessoides*; Table 3).

In many fish stocks, declines in age at maturity have been accompanied by declines in body size at first maturity (Beacham 1983a, b, c, Morgan et al. 1993, O'Brien et al. 1993, Rijnsdorp 1993a). Therefore, not only are fish younger at first reproduction, they are also smaller



Figure 4. Biologist Maria-I. Buzeta holding a large female Atlantic cod captured during a research vessel survey off Nova Scotia in the mid-1980s.

in body size, in some cases 30% smaller than 20 years previously (Beacham 1983a).

Annual monitoring of population parameters such as age at maturity is typically confined to commercially important fish stocks. There are, however, several studies that have compared age at maturity among populations receiving different levels of angling pressure. Results from these studies on northern pike (*Esox lucius*; Diana 1983), brown trout (*Salmo trutta*; Hegge et al. 1991), and Arctic charr (*Salvelinus alpinus*; Hegge et al. 1991) support findings of maturation at a young age in heavily exploited freshwater fish populations.

A physiological limit exists for the age (and length) at which individuals of a species are able to sexually mature. Because significant declines in age at maturity have already been observed, further reductions of the magnitude that occurred in the northwest Atlantic groundfish stocks during the 1960–1980s are no longer possible. In some cases, further reductions may not be physiologically achievable. For example, female cod in the more southern stocks in the northwest Atlantic presently mature at two years of age, and some males mature at age one (Trippel et al. 1995).

Not all fish populations that have declined exhibit lowered age at maturity (Berlinsky et al. 1995, Trippel and Harvey 1987). For example, white sucker (*Catostomus commersoni*) in acidified lakes exhibited late age and large size at sexual maturity despite declines in population size (Trippel and Harvey 1987).

In striped bass (*Morone saxatilis*) in coastal Rhode Island waters, a comparison of the maturity schedule observed from 1985–1987 with that reported after a 1941 investigation indicates that, although population size declined, age at maturity increased slightly (4.6–5.3 years; Berlinsky et al. 1995). Considering that the abundance of this recreationally favored species declined substantially on the east coast of the United States during the 1970s, it is interesting that no downward shift in maturity occurred over this 46-year period.

The consequences of a change in stock size and age structure associated with exploitation but without a compensatory response of lowered age at maturity are potentially critical. It may be that such stocks are severely stressed, because lowered egg production due to depletion of large fish is not compensated by increased egg production by young fish. The ages at maturity of the exploited cod, haddock, and flatfish stocks documented in Tables 1–3 probably do reflect the declining trends in population size they have experienced, but their flexibility to lower age at maturity may help them increase egg production and recover more quickly than would stocks or species with less flexibility

in this life-history trait.

There are many significant issues relevant to the interpretation of shifts in age at maturity. These issues include determination of the cause of early maturity and evaluation of the reproductive potential of a diminished population that exhibits early maturity. Finally, would a reduction in fishing pressure and subsequent increase in population size shift age at first maturity back to older ages?

Causes of early maturity

Most studies support the idea that early maturity is caused by compensatory responses to declining population size and/or by genetic selection. The compensatory response to lowered population size is a purely phenotypic response and is not attributed to changes in genotype. It is to be distinguished from character evolution without plasticity and genetic variation for plasticity (Scheiner 1993, Via and Lande 1985).

Compensatory responses. Declines in age at first maturity have been commonly associated with compensatory responses to a reduction in population size (Figure 5; Colby and Nepsky 1981, Nikol'skii 1962). Compensatory responses are based on density-dependent mechanisms. In theory, a reduction in population size, for example, through harvesting of adult fish, results in lower intraspecific competition. The lower competition provides for greater food intake per individual and thus faster growth. The faster growth enables fish to achieve maturation at a younger age. Evidence for the compensatory theory has been observed in many studies (Alm 1959, Bowering and Brodie 1991, Diana 1983, Healey 1980, Nikol'skii 1962). This shift to an earlier age at maturity presumably is an adaptation to maintain or achieve the maximal reproductive output possible in a lifetime. It also, hypothetically, permits a reduced population to expand in size sooner than if age at reproduction had remained unchanged.

Body size at maturity typically exhibits greater variability in re-

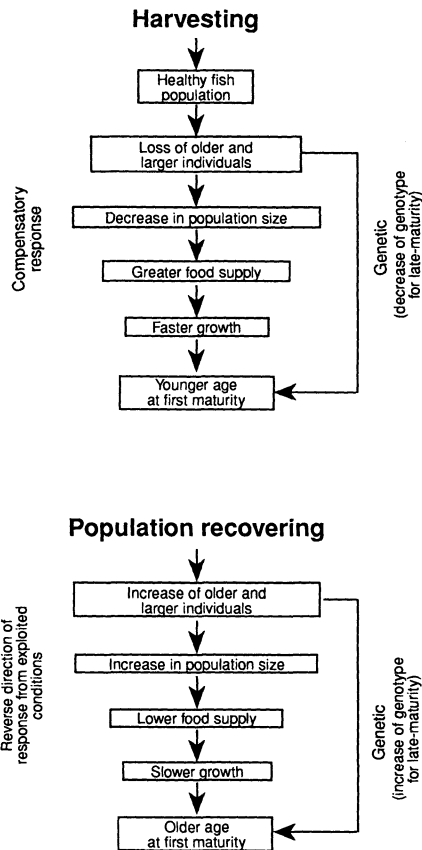


Figure 5. Model descriptions of the mechanisms underlying two key theories: the compensatory response to declining population size and the genetic selection that explains shifts in age at maturity in fish populations. Model steps are shown for the effects of harvesting and for population recovery.

sponse to declines in population size than does age at maturity (Policansky 1993). Fish may attain maturity at either smaller or larger body sizes after a reduction in population size. Larger body size is explained as follows: Fish normally exhibit slow growth when population density is high. At reduced population size, the accelerated growth experienced by maturing individuals could pass them quickly through size ranges that previously necessitated several years of slow growth. The accelerated growth, hypothetically, results in individuals being both larger and younger at maturity than when population size was bigger. For example, Pacific halibut (*Hippoglossus stenolepis*) attained maturity at a larger body size after population reduction (Schmitt and Skud 1978).

However, the majority of the

documented shifts in size at maturity have occurred in the direction of smaller sizes (e.g., Beacham 1983a, b, c, Rijnsdorp 1993a). Is this observation consistent with the compensatory theory? Onset of maturation is sensitive to energy intake or growth during the juvenile phase (Rijnsdorp 1993b, Trippel and Harvey 1989), or more specifically at some critical, relatively short period during this juvenile phase (Burton 1994, Iles 1984, Rowe and Thorpe 1990). Fish may be smaller at maturity if they can acquire at a young age (and a small size) the necessary nutrition to support gonadal maturation.

Other factors governing shifts in maturity may sometimes confound the compensatory response to lowered population size. Consider interspecific competition. A reduction in population size would not affect age at maturity if food supply per individual were not to increase. Another fish species that shares a diet with the species under stress may simply become more abundant. Field experimental tests have confirmed that interspecific competition leads to an increase in age at maturity (Persson 1990). This scenario was also observed in yellow perch (*Perca flavescens*) after the removal of white suckers from a northeastern Minnesota lake (Johnson 1977).

Environmental conditions could also be important. Decreases in water temperature may prevent fish in the depauperate population from realizing their growth potential, because water temperature is a key factor controlling growth metabolism in fishes; different species exhibit different temperature optima (Jobling 1981). Evidence of food limitation, restricted distribution, and the paucity of alternative food sources for fish in small lake ecosystems may increase the likelihood for these populations to exhibit patterns that concur with the compensatory theory (Alm 1959, Diana 1983, Healey 1980).

Fast-growing fish of exploited populations generally have a relatively greater reproductive output than fish in unexploited conditions (i.e., as measured by increases in egg production by fish of a certain size

or age). This greater reproductive output has been shown, for example, for plaice (*Pleuronectes platessa*; Bagenal 1966), lake trout (*Salvelinus namaycush*; Healey 1978), and lake whitefish (*Coregonus clupeaformis*; Healey 1978). This fecundity component of the compensatory response has not been as widely documented as have the growth rate and maturity responses, in part because lengthy time series of fecundity estimates are not frequently developed for fish populations.

Fecundity estimates for cod in the northwest Atlantic have been restricted to the more northern stocks (Pinhorn 1984, Powles 1958). Results indicate significant interyear differences in numbers of eggs produced at a given length or age, though the number of years in which fecundity observations were made for the same area were too few to allow correlation with stock size (Pinhorn 1984). Further research is required to assess the density-dependent mechanisms influencing northwest Atlantic cod fecundity. Cod fecundity estimates have not yet been made for a large number of northwest Atlantic cod stocks including Georges Bank, Bay of Fundy, and the Nova Scotian Shelf. The only existing fecundity estimate for cod south of the Gulf of Saint Lawrence is based on six specimens that have weights of 10 to 35 kg. These weights span the typical body-weight range of mature cod collected in the late-1870s (Earll 1880).

Genetic selection: size-selectivity for early maturity. If age at maturity is a heritable trait (as has been shown for some salmonids; Gjerde 1984, Tipping 1991), then the shift to an earlier age at maturity becomes a function of changes in genotype frequencies in a population over time. In a heavily exploited population, few late-maturing fish are likely to survive to reproduce. In contrast, those fish that mature early in life may participate in one or two breeding seasons before they are captured. Over time, year classes of a stressed population become comprised increasingly of progeny from early maturing fish. The change in gene frequencies over time may partly account for the new maturity pro-

file of the depauperate population. This description is consistent with the more traditional view of character evolution without plasticity.

The mechanism responsible for genetic selection is reflected in the first step of the compensatory theory through heightened mortality, particularly of late-maturing fish that are captured before they first spawn (Figure 5). Maturing at a younger age and smaller size permits fish to participate in spawning before they become vulnerable to fishing gear. By 1716 in England, minimal mesh sizes and minimal size limits for various fish species were in effect, with potentially severe penalties for noncompliance (Policansky 1993). The goal of these regulations was to ensure the selective capture of larger fish. For some fish stocks, the period of fishing has probably exceeded 40 generations, which would be long enough for selection to produce substantial genetic change (Policansky 1993). Evidence for a genetic effect on changes in maturation were reported for female North Sea plaice (Rijnsdorp 1993a), though for Norwegian coastal cod and northeast Arctic cod, environmental factors were considered more important in the understanding of variations in age at maturity (God and Moksness 1987).

Compared with the simplicity of following changes in age at maturity over generations in river runs of Pacific salmon in which individuals die immediately after spawning, for example, coho salmon (*Oncorhynchus kisutch*) and pink salmon (*Oncorhynchus gorbuscha*; Ricker 1981), difficulty exists in properly addressing genetic selection in a multi-age population. For example, the North Sea cod stock is composed of several year classes at any one time, each of which may be experiencing selection, with the selection pressure changing as the fish in that year class grow older. Each year class contributes to the progeny production of new year classes in a manner that depends in part on its relative abundance in the population. Furthermore, the stock is typically far from a demographic steady state with as much as a tenfold variation in year class size annually. Such demographic complexities are typical of multi-age stocks

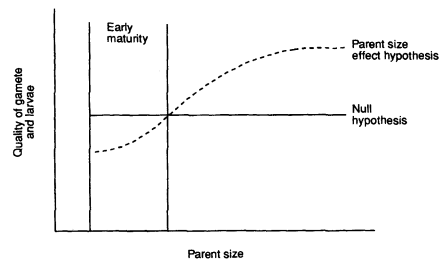


Figure 6. Schematic representation of relationship between parent size, gamete quality, and early maturity. The null hypothesis signifies that gamete quality remains constant with increases in female body size. The parent size effect hypothesis (which is supported for cod and haddock) indicates increases in parental body size have a positive influence on the size or quality of eggs and larvae. The area labeled early maturity represents conditions that may be experienced by a heavily exploited stock.

and to not account for them would be to miss a major factor affecting the response to selection (Law and Rowell 1993).

Evidence contrary to the compensatory theory may assist in building support for the effects of inheritance on age at maturity (Nelson and Soule 1986, Rijnsdorp 1993a). Grand Bank cod were exhibiting decreased size at age (slow growth) and were thinner than normal (low-condition factor) when reductions in age and length at maturity were observed during the early 1990s (Baird et al. 1992, Morgan et al. 1993), aspects contrary to those predicted by the compensatory theory. Fish that were exhibiting early maturity were progeny from the mid-to late 1980s when late maturity was prevalent among stock members. Apparently, the surviving juveniles at the time of the dramatic stock decline in the early 1990s possessed the phenotypic plasticity to produce the observed declines in age and size at maturity (in the absence of an abundance of food). This example lends support to evidence that the genetic influence on age at maturity acts in the form of a capability with rather wide latitude (i.e., phenotypic plasticity) and not by strict age-specific inheritance of age at maturity from parent to progeny (Saunders 1986, Scheiner 1993, Stearns 1992, Via and Lande 1985). Fish species and population mem-

bers may differ in their capacity to exhibit phenotypic plasticity for this response, which could affect their resiliency to exploitation.

The inheritance of adaptive phenotypic plasticity is an important concept and should be distinguished from character evolution without phenotypic plasticity (Scheiner 1993, Via and Lande 1985). Investigators have found difficulty in explaining shifts in age at maturity in fish stocks when confining a large part of their analysis to character evolution without phenotypic plasticity (Law and Rowell 1993). A detailed modeling effort of this kind is warranted for Grand Bank cod.

Empirical and theoretical support for a variety of factors and processes (e.g., lake acidification, lake productivity, and socially induced inhibition) that have influence over age at maturity have been the subject of many other investigations that have not necessarily dealt with overexploited populations (Fox and Keast 1991, Hayes and Taylor 1990, Sohn 1977, Trippel 1993, Trippel and Harvey 1987) and are of potential value in interpreting variations in age at maturity. Age at maturity in male platyfish (*Xiphophorus maculatus*) is an excellent example where the presence of large males socially suppresses maturation in small males (Sohn 1977).

Covariations in age and size at maturity have been examined in recent years (Hutchings 1993, Rijnsdorp 1993b) as have trade-offs among growth, reproduction, and mortality as determinants of the optimal age at maturity (Roff 1983, Stearns 1992, Stearns and Crandall 1984). In Atlantic cod, however, trade-offs in growth due to reproduction are not evident (Trippel et al. 1995, Waiwood 1982). Waiwood (1982) showed that body weight gains by maturing fish were 30%–60% greater than those of immature fish. Mature gonad weight typically makes up 12%–15% of total body weight in cod (Trippel and Morgan 1994).

Understandably, the complexity of interactions that occur in an ecosystem at the individual level during the years preceding maturity make it difficult to pinpoint a single cause of early maturity. Shifts in maturity

are most likely to be a consequence of a mix of factors having both compensatory and genetic origins. To assess the relative role of each factor is likely to depend on future research that endeavors to determine the ability of fish to inherit life-history traits as well as the heritability of the phenotypic plasticity of each trait (Allendorf et al. 1986, Tipping 1991, Via and Lande 1985). A comparative analysis among wild, outbred animals has shown that approximately 25% of the phenotypic variation in life-history traits such as age at maturity is of genetic origin and 75% of environmental origin (this degree of heritability is less than that of morphological traits; Mousseau and Roff 1987).

Despite arguments and evidence that evolution might be occurring in exploited fish populations, fishery managers have not considered it seriously. This reaction is not surprising, as too often it is impossible to show that evolution has occurred or to provide an accurate, plausible prediction of how evolution might occur in the future. In natural populations of long-lived, repeat-spawning fish like cod, the results of fisheries selection are difficult to verify. Policansky (1993) indicated there is a need to develop better programs to detect the effects of evolution in exploited populations and secondly, and perhaps more promising, to conduct computer simulation modeling. Simulations would permit the exploration of various outcomes that certain shifts in genotype may have on the expression of traits like age at maturity. Notwithstanding the difficulties in detection of the causes of the reported declines in age at maturity among many populations worldwide, there has been an emergence of certain reproductive characteristics that suggest special consideration by managers be made when interpreting the reproductive potential of depressed fish stocks.

Reproductive potential

John Hart, former director of the St. Andrews Biological Station in New Brunswick, Canada, summarized the situation with regard to the Atlantic fisheries near the turn of the nineteenth century:

[B]y 1910 people engaged in the fisheries on the Atlantic coast had no clear recollection of former conditions of excessive abundance or of sharp declines in the reward for fishing effort. Supplies of older fishes had already declined. (Hart quoted in Johnstone 1977, p. 22)

During periods when stock sizes were larger and made up of a broad age span the young, first-time spawning fish only made up a small fraction of the total spawning stock biomass. In recent years, first-time spawners make up an increasing proportion of total spawning stock biomass. First-time spawners are commonly detected by their relatively small body size and their achievement of maturity at a young age. Current profiles of ages of spawning segments of southern cod populations are comprised mainly of three- to four-year-olds with a low proportion of fish older than seven years (Trippel et al. 1995). Body sizes are commonly less than 60 cm and less than 3–4 kg. Similarly, in the northeast Arctic cod stock the landed catches by longline gear (baited hooks set along the ocean bottom) in the late 1980s was comprised of approximately 80% virgin fish compared with a level of approximately 50% between 1932–1955 (Jørgensen 1990). If unique reproductive attributes pertaining to large fish exist, then due to the decline in their numbers the prevalence of these spawning traits has been substantially diminished in present-day northwest Atlantic groundfish stocks. Two important reproductive traits that vary as a function of body size are egg size and length of spawning season.

Egg size. In cod and haddock, as individuals increase in body size they produce eggs of larger diameter (for cod an increase of 1.33–1.46 mm in diameter or 38% by volume over a length range of 56–75 cm; for haddock the dry weight of eggs increased by 21% between the ages of two and three years; Hislop 1988, Kjesbu 1989). Laboratory experiments have demonstrated that the larger eggs in turn produce larger larvae, which have stronger activity patterns and higher survival rates than progeny originating from smaller eggs

(Knutsen and Tilseth 1985, Solemdal et al. 1992). Therefore, quality of larvae improves with increases in parent body size (Figure 6). Presently, eggs in many cod stocks are being produced by fish of small body sizes, which decades earlier would have been reproductively inactive. Therefore, besides a reduction in number of eggs spawned by the whole stock, egg size is also reduced in depauperate cod stocks comprised of young fish. It is not known whether small cod are constrained to produce only small eggs or whether that strategy produces more eggs rather than fewer large eggs. For males, an analysis of sperm concentration, motility, and fertilization potency failed to reveal any significant differences between virgin and repeat-spawning male cod (Trippel and Neilson 1992).

Several other fishes, in addition to cod and haddock, also show a positive correlation between offspring viability and parent size: winter flounder (*Pseudopleuronectes americanus*; Buckley et al. 1991), brook trout (*Salvelinus fontinalis*; Hutchings 1993), and striped bass (Zastrow et al. 1989). For example, of relevance to the important striped bass recreational fishery along the coast of New England, 4- to 5-year-old striped bass produced eggs with a 21% lower hatching success than eggs from fish ages 7–15 (Zastrow et al. 1989). Houde et al. (1988, 1989) estimated that 62% and 76% of the striped bass eggs collected in the Potomac River in 1987 and 1988, respectively, were produced by first-time spawners. This percentage is unusual, because striped bass is a long-lived species, and individuals are capable of spawning many times during their life-span. It indicates that older age classes in these spawning runs were scarce.

In largemouth bass (*Micropterus salmoides*) and smallmouth bass (*Micropterus dolomieu*), common freshwater sport fish of North American inland lakes, the more viable progeny result from large parents that start spawning earlier in the year than do the small, young bass (Miranda and Muncy 1987, Ridgway et al. 1991). The earlier spawning by large bass permits the larvae and resulting juveniles to ex-

perience a longer summer growing period, which improves their chances of surviving overwinter conditions, a period when feeding ceases and young-of-the-year depend on critical levels of energy reserves for their survival (Shuter et al. 1980).

Spawning time. For Newfoundland cod in Trinity Bay, a small cod of 50 cm may spawn 370,000 eggs, whereas a large, repeat-spawning cod of 80 cm may spawn 1.6 million eggs, and a 100-centimeter cod 3.2 million (Pinhorn 1984). Large Atlantic cod spawn more batches of eggs and are present on the spawning grounds for a longer period than small cod (Hutchings and Myers 1993, Kjesbu 1989, Trippel and Morgan 1994). With the loss of large, old cod the spawning period in effect has become contracted for the whole stock. Consequently, the delicate adjustments of larval production to the natural production of the plankton could be upset. Predator-prey (i.e., fish-plankton) matches have been considered to increase the rate of survival of marine fish larvae (Lambert 1990). The shortened spawning season of an age-truncated stock presumably results in fewer opportunities for favorable temporal matches of emerging fish larvae and zooplankton prey. Therefore, a stock comprised of individuals with a broad range of body sizes that broadcast eggs over a lengthy spawning period would enhance opportunities for the production of large year classes (Lambert 1990, Lambert and Ware 1984).

On the Grand Banks, the abrupt decline in 1991 of cod in the age range 7 to 20 years to a level of approximately 10% of the long-term average suggests that egg production, timing of spawning, and egg size and viability are critical elements to be considered in assessing probable trends in future population growth of this stock that once provided a yield in excess of 250,000 metric tons annually. These aspects of cod reproduction are influenced by harvesting practices and thus come under some form of management control, while annual variations in water temperature and certain supplies of food are not subject to manipulation of stock structure,

though they are also necessary components in any prediction making for stock recovery rates.

The striped bass recovery along the Atlantic coast is a good example of managers adopting a strategy based on improving a stock's reproductive potential. The management objective was to expand the abundance and age structure of the Chesapeake stock through live release by anglers of large, repeat-spawning striped bass (Boreman and Goodyear 1984), with the hypothesis that this release would increase stock fecundity and the resilience that comes with a broad age structure in a long-lived species (i.e., repeat-spawning potential to compensate for frequent year classes of poor size). For lake trout in northwestern Ontario lakes, restrictions on the harvesting of large lake trout of trophy size have been recommended in order to maintain or enhance egg production (Trippel 1993).

The unique reproductive traits of large cod indicate that spawning-stock biomass estimates do not clearly reflect actual reproductive potential. Further experiments are encouraged to enable investigators to appropriately rank the reproductive value of different age groups of sexually mature fish and not equate similar weights of small and large fish when deriving total spawning stock biomass estimates as is prevalent in the fisheries literature (e.g., Maguire and Mace 1993, Serebryakov 1990). Disregarding the influence of parent size on egg quality and length of spawning season may lead to overestimates of reproductive potential for age-truncated populations when using traditional analytical methods. Young, mature male Atlantic cod may not even participate in spawning activity (Trippel and Morgan 1994). Inappropriate use of spawning stock biomass to represent reproductive potential has been pointed out before (Rothschild and Fogarty 1989) though that approach may be even less accurate than previously believed.

Return to older ages at maturity

Supportive evidence exists for rapid shifts in age at maturity in fish popu-

lations. However, the monitoring of annual changes in age at first maturity as a barometer for estimating fish population size or year class size, in isolation from other population attributes, is not recommended (Figure 5) for several reasons. Shifts in age at maturity may lag behind improved population conditions such that the response may be expressed too slowly to be a useful monitor. Strong year classes may pass through a fishery, increasing the stock biomass, while age at first maturity may remain unchanged. Early age at maturity may in this sense be considered a product or remnant of a process that occurred during a period when stock size was markedly lower. Closer examination of lag time responses may assist in the interpretation of maturity data for estimating population size.

The large increase in stock size of herring (*Clupea harengus*) in the North Sea during the early 1980s provides rare evidence that age at maturity responds rapidly to changes in population size. Specifically, the percentage of two-year-olds that were mature decreased with an increase in stock size (Anonymous 1986). Recent resurgence of the Georges Bank herring stock also is being accompanied by an increase in age at maturity. Since the early stage of recovery in the mid-1980s, the percentage of three-year-olds that were mature has decreased by approximately 50% (Melvin et al. 1995).

To further explore the use of age at maturity as a predictor of population size, I recommend that regression equations be constructed between population size (as well as year class size) and age at maturity for a variety of stocks of different fish species. In some cases, equations may prove to be useful predictive tools; however, caution should be exercised as with any stock size indicator when using age at maturity as a predictor of fish abundance.

Conclusions

Fish stocks worldwide have experienced dramatic declines. Moratoria on fishing have been imposed to allow stocks to rebuild rather than

being fished to extinction. The issues of reproductive capacity are critical to stock rebuilding. Evidence indicates that stocks comprised of fish of a broad range of ages and sizes are able to spawn more eggs of a large range in size and that these eggs are spawned over a longer period of time than eggs produced by stocks comprised primarily of young fish. Management on the basis of reducing fishing pressure to levels that permit fish to reach older ages should be pursued. Rebuilding age structure can most simply be achieved by meeting recommended scientifically based harvest levels (approximately 20% of exploitable stock size) though under some circumstances stock closures may be necessary for rebuilding.

The biological consequences of selective removal of large fish are now more clearly understood, and the excessive removal of fish can no longer be perceived as simply leading to a reduction in the number of eggs produced by a population. Important aspects of egg size and spawning time are also jeopardized by high levels of exploitation. Further studies to evaluate reproductive capacity of stocks are encouraged, so that managers may better predict stock rate increases and make more informed decisions on their exploitation and conservation.

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References cited

- Allendorf FW, Ryman N, Utter FM. 1986. Genetics and fishery management: Past, present and future. Pages 1–19 in Ryman N, Utter F, ed. Population genetics and fishery management. Seattle (WA): University of Washington Press.
- Alm G. 1959. Connection between maturity, size and age in fishes. Report of the Institute of Freshwater Research, Drottningholm 40: 5–145.
- Anonymous. 1986. Report of the Herring Assessment Working Group for the Area South of 62 N. Committee Meeting Assessment: 19. Copenhagen (Denmark): International Council for the Exploration of the Sea. C.M. 1986/Assess: 19.
- _____. 1993. Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) Annual Report, Vol. 15, 1992. Dartmouth (Nova Scotia): Atlantic Stock Assessment Secretariat. Available from: Bedford Institute of Oceanography, Department of Fisheries and Oceans, P. O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.
- _____. 1994. Report on the status of ground-fish stocks in the Canadian Northwest Atlantic, June 1994. Dartmouth (Nova Scotia): Atlantic Stock Assessment Secretariat. Available from: Bedford Institute of Oceanography, Department of Fisheries and Oceans, P. O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.
- Bagenal TB. 1966. The ecological and geographical aspects of the fecundity of the plaice. *Journal of Marine Biology Association of the United Kingdom* 46: 161–186.
- Baird JW, Bishop CA, Brodie WB, Murphy EF. 1992. An assessment of the cod stock in NAFO Divisions 2J3KL. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 92/75. Available from: Bedford Institute of Oceanography, Department of Fisheries and Oceans, P. O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.
- Beacham TD. 1983a. Variability in median size and age at sexual maturity of Atlantic cod (*Gadus morhua*) on the Scotian Shelf in the Northwest Atlantic Ocean. *Fishery Bulletin* 81: 303–321.
- _____. 1983b. Growth and maturity of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Canadian Technical Report of Fisheries and Aquatic Sciences 1142.
- _____. 1983c. Variability in size and age at sexual maturity of haddock (*Melanogrammus aeglefinus*) on the Scotian Shelf in the Northwest Atlantic. Canadian Technical Report of Fisheries and Aquatic Sciences 1168.
- Berlinsky DL, Fabrizio MC, O'Brien JF, Specker JL. 1995. Age at maturity estimates for Atlantic coast female striped bass. *Transactions of the American Fisheries Society* 124: 207–215.
- Boreman J, Goodyear CP. 1984. Effects of fishing on the reproductive capacity of striped bass in Chesapeake Bay, Maryland. Reference Document nr 84-29. Woods Hole (MA): Woods Hole Laboratory.
- Bowering WR, Brodie WB. 1991. Distribution of commercial flatfishes in the Newfoundland-Labrador region of the Canadian Northwest Atlantic and changes in certain biological parameters since exploitation. *Netherlands Journal of Sea Research* 27: 407–422.
- Buckley LJ, Smigleski AS, Halavik TA, Caldaroni EM, Burns BR, Laurence GC. 1991. Winter flounder *Pseudopleuronectes americanus* reproductive success. II. Effects of spawning time and female size on size, composition and viability of eggs and larvae. *Marine Ecology Progress Series* 74: 125–135.
- Burton MPM. 1994. A critical period for nutritional control of early gametogenesis in female winter flounder, *Pleuronectes americanus* (Pisces: Teleostei). *Journal of Zoology (London)* 233: 405–416.
- Colby PJ, Nepsky S. 1981. Variations among stocks of walleye (*Stizostedion vitreum vitreum*): management implications. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1814–1831.
- [CUD] Conservation and Utilization Division. 1993. Status of fishery resources off the northeastern United States for 1993. NOAA Technical Memorandum NMFS-F/NEC-101. Woods Hole (MA): National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center.
- Diana JS. 1983. Growth, maturation, and production of northern pike in three Michigan lakes. *Transactions of the American Fisheries Society* 112: 38–46.
- Earll RE. 1880. A report on the history and present conditions of the shore cod fisheries of Cape Ann, Mass., together with notes on the natural variability and artificial propagation of the species. Pages 685–740 in Report of the commissioner for 1878. Washington (DC): US Commission of Fish and Fisheries.
- Fox MG, Keast A. 1991. Effects of overwinter mortality on reproductive life history characteristics of pumpkinseed (*Lepomis gibbosus*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1792–1799.
- Gjerde B. 1984. Response to individual selection for age at sexual maturity in Atlantic salmon. *Aquaculture* 38: 229–240.
- God OR, Moksness E. 1987. Growth and maturation of Norwegian coastal cod and Northeast Arctic cod under different conditions. *Fisheries Research (Amsterdam)* 5: 235–242.
- Halliday RG. 1987. Size and age of sexual maturity of Atlantic argentine, *Argentina silus*: a critique. *Environmental Biology of Fishes* 19: 139–147.
- Halliday RG, Pinhorn AT. 1985. Present management strategies in Canadian Atlantic marine fisheries, their rationale and the historical context in which their usage developed. Pages 10–33 in Mahon R, ed. Toward the inclusion of fishery interactions in management advice. Canadian Technical Report of Fisheries and Aquatic Sciences No. 1347.
- Hayes DB, Taylor WW. 1990. Reproductive strategy in yellow perch (*Perca flavescens*): effects of diet ontogeny, mortality, and survival costs. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 921–927.
- Healey MC. 1978. Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*). *Journal of the Fisheries Research Board of Canada* 35: 945–950.
- _____. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 255–267.
- Hegge O, Dervo BK, Skurdal J. 1991. Age and size at sexual maturity of heavily exploited Arctic charr and brown trout in Lake Åtnsjø, southeastern Norway. *Transactions of the American Fisheries Society* 120: 141–149.
- Hislop JRG. 1988. The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in Brit-

- ish waters. *Journal of Fish Biology* 32: 923–930.
- Houde ED, Nyman DM, Rutherford ES. 1988. Mortality, growth and growth rate viability of striped bass larvae in Chesapeake subestuaries. Final Report. Reference nr (UMCEES) CBL 88-96. Annapolis (MD): Maryland Department of Natural Resources, Fisheries Division.
- Houde ED, Monteleone DM, Morin GL. 1989. Egg production and larval dynamics of striped bass in the Potomac River and upper Chesapeake Bay. Progress Report. Reference nr (UMCEES) CBL 88-146. Annapolis (MD): Maryland Department of Natural Resources.
- Hunt JJ. In press. Rates of sexual maturation of Atlantic cod in NAFO Division 5Ze and commercial fishery implications. *Journal of Northwest Atlantic Fishery Science* 15.
- Hutchings JA. 1993. Reaction norms for reproductive traits in brook trout and their influence on life history evolution affected by size-selective harvesting. Pages 107–126 in Stokes TK, McGlade JM, Law R, eds. *The exploitation of evolving populations*. Berlin (Germany): Springer-Verlag.
- Hutchings JA, Myers RA. 1993. The effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2468–2474.
- Iles TD. 1984. Allocation of resources to gonad and soma in Atlantic herring *Clupea harengus* L. Pages 331–347 in Potts GW, Wootton RJ, eds. *Fish reproduction strategies and tactics*. London (UK): Academic Press.
- Jobling M. 1981. Temperature tolerance and the final preferendum-rapid methods for the assessment of optimum growth temperatures. *Journal of Fish Biology* 19: 439–455.
- Johnson FH. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. *Journal of the Fisheries Research Board of Canada* 34: 1633–1642.
- Johnstone K. 1977. *The Aquatic explorers: a history of the Fisheries Research Board of Canada*. Toronto (Canada): University of Toronto Press.
- Jørgensen T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *Journal du Conseil International pour l'Exploration de la Mer* 46: 235–248.
- Kjesbu OS. 1989. The spawning activity of cod, *Gadus morhua* L. *Journal of Fish Biology* 34: 195–206.
- Knutsen GM, Tilseth S. 1985. Growth, development and feeding success of Atlantic cod *Gadus morhua* larvae related to egg size. *Transactions of the American Fisheries Society* 114: 507–511.
- Lambert TC. 1990. The effect of population structure on recruitment in herring. *Journal du Conseil International pour l'Exploration de la Mer* 47: 249–255.
- Lambert TC, Ware DM. 1984. Reproductive strategies of demersal and pelagic spawning fish. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1565–1569.
- Law R, Rowell CA. 1993. Cohort-structured populations, selection responses, and exploitation of the North Sea cod. Pages 155–174 in Stokes TK, McGlade JM, Law R, eds. *The exploitation of evolving populations*. Berlin (Germany): Springer-Verlag.
- Mace PM, Sissenwine MP. 1993. How much spawning per recruit is enough? *Canadian Special Publication of Fisheries and Aquatic Sciences* 120: 101–118.
- Maguire J-J, Mace PM. 1993. Biological reference points for Atlantic gadoid stocks. *Canadian Special Publication of Fisheries and Aquatic Sciences* 120: 321–332.
- Melvin GD, Fife FJ, Sochasky JB, Power MJ, Stephenson RL. 1995. The 1995 update on Georges Bank SZ herring stock. Department of Fisheries and Oceans Atlantic Fisheries Research Document 95/86. Available from: Bedford Institute of Oceanography, Department of Fisheries and Oceans, P. O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.
- Miranda LE, Muncy RJ. 1987. Recruitment of young-of-the-year largemouth bass in relation to size structure of the parent stock. *North American Journal of Fisheries Management* 7: 131–137.
- Morgan MJ, Bishop CA, Baird JW. 1993. Temporal and spatial variation in age and length at maturity in 2J3KL cod. *Scientific Council Studies Document* 93/57. Available from: Northwest Atlantic Fisheries Organization, P. O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.
- Mousseau TA, Roff DA. 1987. Natural selection and the heritability of fitness components. *Heredity* 59: 181–198.
- Nelson K, Soule M. 1986. Genetical conservation of exploited fishes. Pages 345–368 in Ryman N, Utter F, eds. *Population genetics and fishery management*. Seattle (WA): University of Washington Press (Washington Sea Grant Program).
- Nikol'skii GV. 1962. On some adaptations to the regulation of population density in fish species with different types of stock structure. Pages 265–282 in LeCren ED, Holdgate MW, eds. *The exploitation of natural animal populations*. Oxford (UK): Blackwell Scientific Publications.
- O'Brien L, Burnett J, Mayo RK. 1993. Maturation of nineteen species of finfish off the northeast coast of the United States, 1985–1990. Technical Report NMFS 113. Woods Hole (MA): National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Center.
- Penttilä J, Dery LM, eds. 1988. Age determination methods for Northwest Atlantic species. Technical Report nr 72. Woods Hole (MA): National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Center.
- Persson L. 1990. A field experiment on the effects of interspecific competition from roach, *Rutilus rutilus* (L.), on age at maturity and gonad size in perch, *Perca fluviatilis* L. *Journal of Fish Biology* 37: 899–906.
- Pinhorn AT. 1984. Temporal and spatial variation in fecundity of Atlantic cod (*Gadus morhua*) in Newfoundland waters. *Journal of Northwest Atlantic Fishery Science* 5: 161–170.
- Policansky D. 1993. Fishing as a cause of evolution in fishes. Pages 2–18 in Stokes TK, McGlade JM, Law R, eds. *The exploitation of evolving populations*. Berlin (Germany): Springer-Verlag.
- Powles PM. 1958. Studies of reproduction and feeding of Atlantic cod (*Gadus callaris* L.) in the southwesten Gulf of St. Lawrence. *Journal of the Fisheries Research Board of Canada* 15: 1383–1402.
- Ricker WE. 1981. Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1636–1656.
- Ridgway MS, Shuter BJ, Post EE. 1991. The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieu* Lacépède (Pisces, Centrarchidae). *Journal of Animal Ecology* 60: 665–681.
- Rijnsdorp AD. 1993a. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia* 96: 391–401.
- _____. 1993b. The relation between juvenile growth and the onset of sexual maturity of female North Sea plaice, *Pleuronectes platessa* L. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 1617–1631.
- Roff DA. 1983. An allocation model of growth and reproduction in fish. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1395–1404.
- Rothschild BJ, Fogarty MJ. 1989. Spawning stock biomass: a source of error in recruitment/stock relationships and management advice. *Journal du Conseil International pour l'Exploration de la Mer* 45: 131–135.
- Rowe DK, Thorpe JE. Suppression of maturation in male Atlantic salmon (*Salmo salar* L.) parr by reduction in feeding and growth during spring months. *Aquaculture* 86: 291–313.
- Saunders RL. 1986. The scientific and management implications of age and size at sexual maturity in Atlantic salmon (*Salmo salar*). *Canadian Special Publication Fisheries and Aquatic Sciences* 89: 3–6.
- Scheiner SM. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* 24: 35–68.
- Schmitt CC, Skud BE. 1978. Relation of fecundity to long-term changes in growth, abundance and recruitment. *Science Report* nr 66. Seattle (WA): International Pacific Halibut Commission.
- Scott WB, Scott MG. 1988. Atlantic fishes of Canada. *Canadian Bulletin of Fisheries and Aquatic Sciences* 219.
- Serebryakov VP. 1990. Prediction of year-class strength under uncertainties related to survival in early life history of some north Atlantic commercial fish. NAFO SCR Doc. 90/115. Available from: Northwest Atlantic Fisheries Organization, P. O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.
- Shuter BJ. 1990. Population-level indicators of stress. Pages 145–166 in Adams SM, ed. *Biological indicators of stress in fish stocks*. American Fisheries Society Symposium 8: 145–166.
- Shuter BJ, MacLean JA, Fry FEJ, Regier HA. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth

- bass. *Transactions of the American Fisheries Society* 109: 1–34.
- Sinclair A. 1993. Report on the assessments of groundfish stocks in the Canadian Northwest Atlantic, May 4–14, 1993. Canadian Technical Report on Fisheries and Aquatic Sciences nr 1946.
- Sohn JJ. 1977. Socially induced inhibition of genetically determined maturation in the platyfish, *Xiphophorus maculatus*. *Science* 195: 199–200.
- Solemdal P, Bergh O, Finn RN, Fyhn HJ, Grahl-Nielsen O, Homme O, Kjesbu OS, Kjorsvik E, Opstad I, Skiftesvik AB. 1992. The effects of maternal status of Arcto-Norwegian cod on egg quality and vitality of early larvae. II. Preliminary results of the experiment in 1992. Committee Meeting 1992/G:79—Demersal Fish Committee, Ref. L—Biological Oceanography Committee. Copenhagen (Denmark): International Council for the Exploration of the Sea.
- Spangler GR, Payne NR, Byrne JE, Regier HA, Christie WJ. 1977. Responses of percids to exploitation. *Journal of the Fisheries Research Board of Canada* 34: 1983–1988.
- Stearns SC. 1992. *The evolution of life histories*. New York: Oxford University Press.
- Stearns SC, Crandall RE. 1984. Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. Pages 2–33 in Potts GW, Wootton RJ, eds. *Fish reproduction: strategies and tactics*. New York: Academic Press.
- Taylor WW, Smale MA, Brown RW. 1992. Evaluation of size versus age dependent maturation of lake whitefish stocks in the upper Great Lakes. *Polish Archives of Hydrobiology* 39: 269–277.
- Tipping JM. 1991. Heritability of age at maturity in steelhead. *North American Fisheries Management* 11: 105–108.
- Trippel EA. 1993. Relations of fecundity, maturation, and body size of lake trout, and implications for management in northwestern Ontario lakes. *North American Journal of Fisheries Management* 13: 64–72.
- Trippel EA, Harvey HH. 1987. Reproductive responses of five white sucker (*Catostomus commersoni*) populations in relation to lake acidity. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 1018–1023.
- _____. 1989. Missing opportunities to reproduce: an energy dependent or fecundity gaining strategy in white sucker (*Catostomus commersoni*)? *Canadian Journal of Zoology* 67: 2180–2188.
- _____. 1991. Comparison of methods used to estimate age and length of fishes at sexual maturity using populations of white sucker (*Catostomus commersoni*). *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1446–1459.
- Trippel EA, Morgan MJ. 1994. Age-specific paternal influences on reproductive success in Atlantic cod (*Gadus morhua*) of the Grand Bank, Newfoundland. *International Council for the Exploration of the Sea Marine Science Symposium* 198: 414–422.
- Trippel EA, Neilson JD. 1992. Fertility and sperm quality of virgin and repeat-spawning Atlantic cod (*Gadus morhua*) and associated hatching success. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2118–2127.
- Trippel EA, Buzeta M-I, Hunt JJ. 1995. Evaluation of the cost of reproduction in Georges Bank Atlantic cod (*Gadus morhua*): utility of otolith back calculation. Pages 599–616 in Secor DH, Dean JM, Campana SE, eds. *Recent developments in fish otolith research*. Columbia (SC): University of South Carolina Press.
- Via S, Lande R. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39: 505–522.
- Waiwood KG. 1982. Growth history and reproduction in Atlantic cod (*Gadus morhua*). Pages 206–208 in Richter CJ, Goos HJT, eds. *Proceedings of the International Symposium on Reproductive Physiology of Fish*; Wageningen, the Netherlands, 2–6 Aug 1982. Wageningen (the Netherlands): Pudoc.
- Zastrow CE, Houde ED, Saunders EH. 1989. Quality of striped bass, (*Morone saxatilis*) eggs in relation to river source and female weight. *Rapports et Proces-Verbaux des Reunions Conseil International de l'Exploration de la Mer* 191: 34–42.

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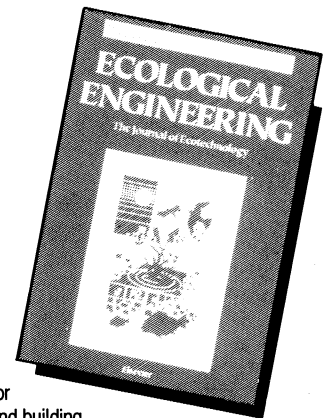
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