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Deep-sea fishes in Canada's Atlantic: population declines and predicted recovery times

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Abstract Because of their slow growth rates, late maturity, low fecundity and long potential lifespans, deep-sea fishes are vulnerable to and theoretically slow to recover from overexploitation and bycatch. As industrial fishing moved into the deep sea, population declines were predicted and five species were shown to meet The World Conservation Union (IUCN) criteria for endangered species in Atlantic Canadian waters and two other deep-living species were listed as threatened by the Committee on the Status of Endangered Wildlife in Canada. We used data from scientific surveys to determine population trends in a 17-year time series for an additional 32 deep-sea fishes from the same geographic region. Eight species exhibited significant population declines, five increased, two were data deficient, and 17 showed no significant trends. Thus approximately 38% of the deep-sea bottom-living fishes in that well-investigated region could be at-risk, but definitive assignment to an IUCN category for most species is hampered by a lack of basic biological information, especially species specific generation times. Lack of biological information also limits efforts to determine possible recovery times, especially with respect to calculating intrinsic rates of population growth (r). For two Atlantic grenadiers (where r could be estimated using life-history parameters and standard life table techniques), the time to recovery with no fishing mortality could range from over a decade to over a century. This broad range results from the general uncertainty on life-history characteristics of these deep-sea species. Given the documented declines, the lack of basic data on life-history parameters, and the conservative assumption that recovery rates are likely to be prolonged, we argue that it is imperative to conduct additional studies pertaining to life history characteristics of deep-sea fishes and implement conservation measures in the deep sea immediately.

Keywords Life history parameters · Grenadiers · Intrinsic rate of increase · Endangered species

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Introduction

Conservation in the deep-sea is in its infancy relative to terrestrial and shallow-water ecosystems. Nonetheless, the expanding footprint of fisheries and associated improvements in fishing technology have increased concern over the vulnerability of deep-sea species to overexploitation and loss as bycatch (Koslow et al. 2000; Roberts 2002). In the North Atlantic, the mean fishing depth has increased steadily since 1990 at a rate of 32.1 m per decade (Morato et al. 2006) and currently, 40% of trawling grounds in the world lie deeper than the continental shelves (Roberts 2002).

Despite limited knowledge on the biology of many deep-sea fishes, there are examples of species that are known to be of concern. The Atlantic wolffish (*Anarhichas lupus*), a slow-growing, late-maturing, territorial fish whose populations in the western North Atlantic had declined over 80%, was declared a Canadian species-at-risk in 1999 (O'Dea and Haedrich 2001). Two other wolffish (*A. minor* and *A. denticulatus*) and cusk (*Brosme brosme)* were subsequently listed as Threatened, the grenadier *Macrourus berglax* was listed as Special Concern (COSEWIC 2007) and the grenadier *Coryphaenoides rupestris* was listed as Endangered (COSEWIC 2008). Devine et al. (2006) showed that abundances of five species of deep-sea fishes (*Antimora rostrata, Bathyraja spinicauda, Coryphaenoides rupestris, Macrourus berglax* and *Notacanthus chemnitzi*) from the same geographic area had declined to such an extent that they met The World Conservation Union (IUCN) criteria for endangered. Using IUCN criteria, a species is considered endangered if it has declined >70% over 10 years or 3 generations (whichever is longer) and the causes of the reduction have ceased, are understood, and are reversible (IUCN 2001). The species listed above could be assessed because there were adequate time-series survey data and the generation time of most were known or could be estimated.

Many other deep-sea fishes have characteristics that potentially make them vulnerable (Merrett and Haedrich 1997; Koslow et al. 2000), but assessment is hampered by a lack of basic biological information. Generation time, for example, is unknown for most. Deep-living fish assemblages display less dominance diversity than assemblages that live at shelf depths. Deep-sea fisheries, which represent the major agent of anthropogenic disturbance to deep-sea environments (Roberts 2002; Morato et al. 2006), inevitably capture species other than those they have targeted, and therefore cause significant bycatch mortality (Gordon et al. 1995; Clark et al. 2000; Piñeiro and Bañón 2001). It is therefore reasonable to expect that deep-sea species other than the nine already documented in the western North Atlantic might also qualify as species-at-risk.

There is a need to focus on population rebuilding and future recovery (Safina et al. 2005). The same characteristics that make deep-sea species vulnerable to depletion should also make any recovery slow. Life-history traits typical of deep-sea fishes, such as large body size, slow-growth, and late maturity are significantly correlated to slower maximum population growth rates (Denney et al. 2002). Recovery times have been estimated for sharks (Simpfendorfer 2000) and other fishes (Safina et al. 2005) using basic life-history characteristics and population information.

The purposes of this paper are three-fold. First, we estimate what fraction of the deep-sea demersal fishes in the Northwest Atlantic display population declines that are sufficient to potentially place them in at-risk categories. Based on that analysis, we then estimate recovery times (where possible) for declining species using estimated potential rates of increase (as inferred from published data on their biology). Lastly, we investigate the sensitivity of recovery time to minimal fishing mortality.

Methods

Declines

The East Coast North American Strategic Assessment Project (ECNASAP) database (Brown et al. 1996) was employed as the best available scientific survey time series because it has been checked and vetted by a group of experts from Canada and the US, standardized with respect to tows (gear, duration, and methods), extends to 1500 m, and has been made available to researchers. A depth-stratified random sampling design only began in 1978, so the time series included in the analysis encompassed 17 years starting from that date.

Species were considered 'deep sea' if they were listed as such in the atlas of North Atlantic fishes (Haedrich and Merrett 1988) or are well-known deep-water species (Froese and Pauly 2007). In order to be considered, fish species had to have been collected in more than half of the survey years. These selection criteria resulted in a list of 32 species.

The dataset was screened so that only consistently sampled strata were retained for analysis (as recommended by Hilborn and Walters 1992). Thus, analyses were limited to strata that were sampled in 9 or more years and in at least two of the first and last 5 years of the survey. Number of fish per tow weighted by the geographic area of the stratum was used as an index of relative abundance. For each species the log of the mean value for each year was analyzed over the 17-year time series using robust regression. The percent population change was calculated as

$$\text{Population change} = 100\left(1 - e^{(b*17)}\right)$$

where b is the slope of the regression of fish per tow on year. Based on these results, the species was designated in one of five categories: decline, non-significant decline, increase, non-significant increase, or data deficient.

Intrinsic rate of population growth (r)

The intrinsic rate of increase (r) quantifies how much a population can increase in a given time period. Information pertaining to life-history characteristics for all species that exhibited declines was collected from various sources, including peer-reviewed articles [e.g. Gordon and Mauchline (1996) and Nash and Geffen (2005)] and discussions with researchers from various institutions (e.g. Woods Hole Oceanographic Institution, Flødevigen Marine Research Station) to determine if r could be estimated. If this information was not available, life-history traits were estimated using life-history data for closely-related species wherever possible. All life-history characteristics that were collected were for females.

The estimate of r was calculated for species with adequate age-specific life history information using standard life table techniques (e.g. Simpfendorfer 2000; Krohne 2001). Specifically, they were estimated using the Euler equation, where x is age in years, l_x is survival to age x, and m_x is the expected female offspring for one female at age x:

$$\sum e^{-rx} l_x m_x = 1.0$$

Survival from age 0 to 1 is unknown for most deep-sea species. However, Anderson (1984) found that less than 1% of redfish larvae survived from April through July on Flemish Cap, Newfoundland. These early and rapid declines are common in fish populations (Cushing 1974) and therefore 1% survival from age 0 to 1 was used for the majority of trials to determine r. This approximation most likely underestimates mortality in the first year. Mortality past age 1 was calculated using two common techniques: $\ln(Z) = 1.44 - 0.982 * \ln(w)$ (Hoenig 1983) and $M = 1.6 * K$ (Jensen 1996) where Z is total mortality (natural mortality + fishing mortality), w is maximum age (years), M is natural mortality, and K is the von Bertalanffy growth parameter.

Macrourus berglax

Age specific length and maturity relationships were outlined by Murua (2003). These were considered the best available data for this species and were thus used for this analysis. Whenever possible, data and relationships specific to the bottom survey (1991–2001) were used (rather than commercial data, which presumably targets specific size classes) to minimize sampling bias.

The coefficients of the von Bertalanffy growth curves (in particular K) varied among survey years. The two extreme values (0.062, 0.024) and the mean (0.038) of K were used to estimate mortality.

Murua (2003) recorded the maximum age of *M. berglax* to be near 28 years and age at first maturity as 11 years. The proportion of mature females at a given age was found by the following equation from Murua (2003):

$$\text{Mature proportion} = e^{[-18.785+(1.205x)]}\left(1 + e^{[-18.785+(1.205x)]}\right)^{-1}.$$

Total fecundity at a given age was also calculated using a relationship highlighted by Murua (2003):

$$\text{Total fecundity} = 1401.5\, e^{0.132x}$$

Although the sex ratio of *M. berglax* is known to change with age (Murua 2003), it was assumed to be 1:1 at age 0. The reproductive periodicity (*RP*) of *M. berglax* is unknown, but energy budgets show that some grenadiers may not reproduce on an annual basis and could even be semelparous (Drazen 2002; Drazen 2008). As a result, r was estimated for *M. berglax* assuming that mature individuals spawned every year, individuals spawned every other year (*RP* = 2), and individuals only spawned once at their maximum reproductive potential (19 years of age).

Coryphaenoides rupestris

The maximum recorded age for *C. rupestris* is approximately 60 years and the age of first maturity, 50% maturity, and 100% maturity are thought to be near 6, 10, and 16 years, respectively (Bergstad 1990). The relationship between age and L was found using von Bertalanffy growth-curve terms $K = 0.100$, $L_\infty = 18.1$ cm, and $x_o = -0.9$, where L_∞ is asymptotic pre-anal length (cm), and x_o is the theoretical age when length is zero (Bergstad 1990). Growth coefficients equal to 0.100, 0.086, and 0.114 were used to estimate mortality (Bergstad 1990).

Fecundity at a given length was calculated using the following equation from Allain (2001):

$$\mathrm{Log}\,(\mathrm{fecundity}) = 3.4 * \mathrm{Log}(L) - 0.09$$

The proportion of mature females at a given age was approximated using the relationship shown by Bergstad (1990).

The sex ratio of *C. rupestris* was assumed to be 1:1 at age 0. *RP* is also debated for *C. rupestris* so various scenarios were used, similar to those used for *M. berglax*. The age of maximum reproductive potential for *C. rupestris* is 16 years.

Recovery times

Estimated population declines and their 95% confidence limits from Devine et al. (2006) were used with

Table 1 Deep-water species that occur in 9 or more years of the 17-year ECNASAP database 1978–1994, the number of years each appeared, status as suggested by this study, rate of population change over 17 years, 95% confidence intervals of that estimate, and total number of specimens collected. NS denotes non-significant and DD denotes data deficient

Scientific name	Years	Status	Rate	95% conf intervals	Specimens
Careproctus ranula	9	Decline	98.7	71.8–99.9	134
Lycenchelys sp.	11	Decline	99.2	91.6–99.9	278
Lycodes esmarki	17	Decline	82.5	66.5–90.9	848
Lycodes reticulatus	17	Decline	75.1	48.2–88.0	26 060
Lycodes vahli	17	Decline	72.8	34.5–88.6	35 301
Merluccius albidus	15	Decline	95.2	55.8–99.4	1864
Polyacanthonotus rissoanus	10	Decline	95.0	6.8–99.7	116
Synaphobranchus kaupi	16	Decline	78.1	35.4–92.6	2243
Argentina silus	16	NS decline	24.6		135 934
Bathylagus euryops	15	NS decline	41.0		189
Bathytroctes sp.	13	NS decline	90.3		717
Cottunculus sp.	11	NS decline	55.4		960
Cottunculus thomsoni	14	NS decline	52.1		75
Dibranchus atlanticus	11	NS decline	58.2		48
Micromesistius poutassou	11	NS decline	30.8		161
Myxine glutinosa	11	NS decline	45.1		3459
Nezumia bairdii	17	NS decline	28.8		68 475
Zenopsis conchifera	11	NS decline	28.3		47
Boreogadus saida	17	Increase	77.7	10.2–94.5	115 121
Centroscyllium fabricii	16	Increase	71.8	45.5–85.4	142 853
Helicolenus dactylopterus	16	Increase	95.0	86.5–98.1	2691
Phycis chesteri	16	Increase	68.2	0.05–89.9	57 117
Somniosus microcephalus	13	Increase	78.9	75.9–81.4	39
Artediellus sp.	17	NS increase	26.0		2645
Chlorophthalmus agassizi	11	NS increase	77.9		304
Cottunculus microps	17	NS increase	56.6		2013
Serrivomer beani	17	NS increase	7.3		429
Simenchelys parasiticus	13	NS increase	73.4		138
Trachyrhynchus murrayi	15	NS increase	25.1		8874
Triglops murrayi	16	NS increase	8.0		24 431
Dipturus laevis	15	DD		3 occurrences	192
Harriotta raleighana	10	DD		1 occurrence	16

Table 2 Life-history characteristics of species that have declined significantly. α is the estimated age (years) at 50% maturity and *w* is the estimated maximum age (years)

Species	α (years)	*w* (years)	Fecundity	References
Careproctus ranula	–	–	10–20	Able and Irion (1985)
Lycenchelys sp.	3–5	6+	20–40	Nash and Geffen (2005)
Lycodes esmarki	–	–	1200	Andriashev (1986)
Lycodes reticulatus	–	–	–	
Lycodes vahli	–	–	18–93	Andriashev (1986); Nash (1986)
Merluccius albidus	–	–	340,000	Klein-MacPhee (2002)
Polyacanthonotus rissoanus	–	–	2,000–60,000	Crabtree et al. (1985); Coggan et al. (1998)
Synaphobranchus kaupi	–	8 (?)	111,507–119,467	Gordon and Mauchline (1996); Gordon (2004)
Antimora rostrata	~13	23	–	Magnusson (2001)
Bathyraja spinicauda	12	50	47	Frisk et al. (2002)
Coryphaenoides rupestris	10	60	8,700–56,000	Alekseyev et al. (1992); Kelly et al. (1997)
Macrourus berglax	13–16	28	8,500–79,220	Murua and Motos (2000); Murua (2003)
Notacanthus chemnitzi	–	–	9,000–30,000	Gordon (2004)
Anarhichas denticulatus	5	14	27,000	Gusev and Shevelev (1997); COSEWIC (2001)
Anarhichas lupus	8–10	20	–	O'Dea and Haedrich (2003)
Anarhichas minor	7–10	21	19,000	Gusev and Shevelev (1997); O'Dea and Haedrich (2001)
Brosme brosme	7		1,000,000	Oldham (1972); COSEWIC (2003)

the intrinsic rates of increase in a Schaefer model (Schaefer 1954) to estimate recovery time for each species (similar to Safina et al. 2005). The magnitude of the population decline identified by Devine et al. (2006) was considered to indicate a similar change in biomass (Moss 2002). The first trial assumed that all fishing mortality and disturbances were removed from the system. But a total absence of fishing mortality and disturbances are highly unlikely, so recovery time was also estimated assuming an arbitrary fishing loss of only 5% total biomass annually. This is equivalent to annual harvest rates of Atlantic cod (*Gadus morhua*) off Newfoundland during the 16th and 18th centuries and was meant to represent fishing mortality related to bycatch or a low level of disturbance (Rose 2004). In comparison, annual harvest rates for Atlantic cod exceeded 45% in the early 1990s during heavy exploitation (Rose 2004).

Table 3 Estimates of mortality for *M. berglax* and *C. rupestris* based on published models. *K* is the Von Bertalanffy growth curve coefficient and *w* is the maximum age (years)

Species	Model	Parameters	Estimate of mortality
M. berglax	Hoenig (1983)	$w = 28$	0.1600
	Jensen (1996)	$K = 0.027$	0.0432
	Jensen (1996)	$K = 0.062$	0.0992
	Jensen (1996)	$K = 0.038$	0.0608
C. rupestris	Hoenig (1983)	$w = 60$	0.0757
	Jensen (1996)	$K = 0.100$	0.1600
	Jensen (1996)	$K = 0.086$	0.1376
	Jensen (1996)	$K = 0.114$	0.1824

Table 4 Estimates of intrinsic rates of increase and recovery time, based on possible life-history characteristics of *M. berglax* and estimated declines (mean and 95% confidence intervals) from Devine et al. (2006). *M* is estimated mortality past age 1, l_1 is estimated survival to age 1, *RP* is reproductive periodicity, and *r* is the calculated intrinsic rate of increase. These results assume there are no fishing impacts

M	l_1	*RP*	*r*	Recovery time (years) for population decline estimates		
				Lower CI 80.4%	Mean 88.1%	Upper CI 94.1%
0.1600	0.01	1	0.2020	42	45	49
0.1600	0.01	2	0.1655	52	56	61
0.1600	0.01	Once (x=19)	0.0820	107	115	125
0.1600	0.1	1	0.3296	25	27	29
0.0432	0.01	1	0.3126	26	28	31
0.0432	0.01	2	0.2762	30	32	36
0.0432	0.1	1	0.4397	18	19	22
0.0608	0.01	1	0.2960	28	30	33
0.0608	0.01	2	0.2595	32	35	38
0.0608	0.1	1	0.4231	19	20	22
0.0992	0.01	1	0.2596	32	35	38
0.0992	0.01	2	0.2231	38	41	45
0.0992	0.1	1	0.3869	21	22	25

Results

Declines

Eight species declined significantly over 17 years, five increased, seventeen had no significant temporal trend (of those 10 indicated a non-significant decline and the others had a non-significant increase), and two were data deficient, i.e. insufficient data to make an assessment (Table 1). For those species that had significant declines, the rates ranged from 73 to 99% but confidence intervals for some were quite broad. Nonetheless, declines in four species were clearly in excess of 50% that could qualify them as candidates for Endangered status under IUCN guidelines.

Recovery times

After an extensive investigation, it was determined that length/age data were available for only a very few of the fishes that had declined. In most cases, the species had never been aged and therefore age at maturity, maximum age, and fecundity as a function of age could not be determined or even estimated (Table 2). Even fewer species had associated age-related, life-history parameters needed to create life history tables, and thereby estimate *r*. Thus, *M. berglax* and *C. rupestris* were the only species that could be studied in detail.

Natural mortality estimates for *M. berglax* varied greatly depending on *K* and ranged from 0.0432 to

Table 5 Recovery time (years) for *M. berglax* and *C. rupestris* based on several potential values of *r* and estimated population declines. These results assume a fisheries catch equal to 5% of the total population

Species	*r*	Decline	Proportion of original population reached	Recovery time (years)
M. berglax	0.2020	88.1%	75.2%	53
	0.0820	94.1%	39.0%	248
	0.2762	88.1%	81.9%	39
	0.4397	80.4%	88.6%	19
C. rupestris	0.5681	88.4%	91.2%	16
	0.2787	96.4%	82.1%	50
	0.2420	96.4%	79.3%	49
	0.1570	99.4%	68.2%	136

0.0992 (Table 3). Z was estimated as 0.1600 using the model from Hoenig (1983). Values of M, l_1, and RP were varied to determine the range of possible values for r, which ranged from 0.0820 to 0.4397. Recovery time for *M. berglax* was estimated to be between 18 and 125 years (Table 4). When a catch of 5% was included in the model to account for bycatch in deep-sea fisheries that target other species, the estimated time to recovery ranged from 19 to 248 years (Table 5).

C. rupestris natural mortality estimates ranged from 0.1376 to 0.1824 (Table 3), but Z was estimated to be only 0.0757. The estimates of r for this species also varied greatly depending on the range of parameters used in the life table (Table 6). The recovery times when fishing loss was not included in the model ranged from 14 to 80 years. When catch was set at 5%, the estimated time to recovery ranged from 16 to 136 years (Table 5).

Discussion

Four species had decline rates that exceeded 50% over the 17-year period. Although the generation times of these species are unknown, they most likely would be classified as Endangered or Threatened using IUCN criteria (IUCN 2001).

We expected that the species most likely to show declines would be those that are large and easily caught, including *Phycis* and especially the shark *Centroscyllium fabricii*. In fact, those species closest to this description actually increased in abundance. Declines were observed primarily in small species with habits and lifestyles tied closely to the substrate (i.e. *Careproctus, Lycenchelys* and *Lycodes*). Assuming that fishing activities represent the most serious recent perturbation in the deep Canadian Atlantic, the implication is that habitat disruption has had at least as great an impact on population trends as has direct removal in bycatch.

Trawling is known to drastically change the benthic habitat, resulting in a more homogenous environment (Watling and Norse 1998; Koslow et al. 2001). Although little is known about the association and importance of corals for deep-sea fishes in the Northwest Atlantic, deep-water corals are thought to play an important role in ecosystem structure (Husebø et al. 2002). These corals are easily damaged by trawling and have very slow growth rates and thus recovery times. If their presence is important for the survival of the fishes that have exhibited declines, recovery times for fishes could be on the order of centuries, if they are even possible.

There is insufficient data for the deep-sea species that declined in Canada's Atlantic Ocean to generate precise life tables and recovery-time estimates. This data gap highlights the drastic lag of science in relation to present-day disturbances and the need for

Table 6 Estimates of intrinsic rates of increase and recovery time, based on possible life-history characteristics of *C. rupestris* and the estimated declines (mean and 95% confidence intervals) from Devine et al. (2006). M is estimated mortality past age 1, l_1 is estimated survival to age 1, RP is reproductive periodicity, and r is the calculated intrinsic rate of increase. These results assume no fishing impacts

M	l_1	RP	r	Recovery time (years) for population decline estimates		
				Lower CI 88.4%	Mean 96.4%	Upper CI 99.4%
0.0757	0.01	1	0.3559	25	29	35
0.0757	0.01	2	0.2989	30	35	42
0.0757	0.01	Once (x=16)	0.1570	59	68	80
0.0757	0.1	1	0.5681	14	17	21
0.160	0.01	1	0.2787	32	37	45
0.160	0.01	2	0.2214	41	47	57
0.160	0.1	1	0.4922	17	20	25
0.1376	0.01	1	0.2992	30	35	42
0.1376	0.01	2	0.2420	38	43	52
0.1376	0.1	1	0.5124	16	19	24
0.1824	0.01	1	0.2582	35	40	48
0.1824	0.01	2	0.2008	46	53	62
0.1824	0.1	1	0.4720	18	21	26

more extensive research in the deep sea (Haedrich et al. 2001). Deep-sea fishes (including those that are not economically important) should be aged and studied in detail to determine the possible indirect influences of human activities.

The values of *r* and recovery time for *C. rupestris* and *M. berglax* were wide-ranging and can only be considered ‘soft’ estimates. Nonetheless, given that the deep-sea fishery had already begun off Canada by 1978 (Haedrich et al. 2001), the target for recovery used in this analysis is most likely an underestimate. Moreover, the ‘known’ life-history parameters for these deep-sea fishes have likely changed as a result of recent disturbances and therefore do not represent those of a pristine population.

When minimal fishing mortality was included in the model, the estimated times to recovery increased. There are few areas in the world where disturbance and fishing mortality are absent, even in the deep sea; thus the estimates that include fishing mortality are probably more realistic. Although *C. rupestris* and *M. berglax* are no longer targeted fisheries in Atlantic Canada, other deep-sea fisheries still occur and bycatch could remain a problem.

Future management decisions should be based on strong science and the precautionary principle. The burden of proof should be reversed to prevent fisheries from being developed without first understanding the basic biology of the target species and those that will be caught as bycatch. In the meantime, large no-take marine protected areas should be created to not only protect the target species, but also habitat. These prudent measures would help ensure that ignorance is not used an excuse for causing long-lasting effects in the deep-sea ecosystem. The results clearly show that any conservation measure established for the deep-sea ecosystem could be slow to demonstrate significant results, so action should be taken quickly and lack of instant results should not be justification for discontinuing conservation initiatives.

Conclusions

Many of the basic life-history characteristics needed to manage fish populations are not yet known for deep-sea fishes and, although most species are not targeted by directed fisheries, almost 40% of the species examined declined over a time period of only 17 years. This research shows that significant declines have already occurred and reversal could take more than a century, if reversible at all. Research is urgently needed to ensure appropriate management strategies are developed for deep-sea fishes.

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