

Effective size closely approximates the census size in the heavily exploited western Atlantic population of the sandbar shark, *Carcharhinus plumbeus*

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Abstract The sandbar shark, *Carcharhinus plumbeus*, is a long-lived species with low lifetime fecundity that is heavily fished in the western North Atlantic. Inshore nursery grounds increase survivorship of sandbar shark pups and the principal nurseries are in the mid-Atlantic region. We calculated effective number of breeders (N_b) and effective population size (N_e) for adults utilizing the nursery grounds of the Delaware Bay and the Eastern Shore of Virginia by genotyping 902 animals across five cohorts at eight microsatellite loci. Estimates of N_b and N_e were compared to estimates of census size (N_c) of cohorts obtained from Delaware Bay. The estimated N_e/N_c and N_b/N_c ratios were 0.45 or higher whether the Delaware Bay cohorts were considered as distinct year classes or combined. This is in contrast to estimated N_e/N_c ratios in other exploited marine fishes, which are several orders of magnitude smaller. Instead, the N_e/N_c ratio of sandbar sharks is similar to that found in marine and terrestrial mammals.

Keywords Effective population size · Effective number of breeders · Elasmobranchs · Microsatellites · Linkage disequilibrium · Temporal method

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Introduction

Effective population size (N_e) is an important consideration for wildlife conservation and management because it is inversely proportional to the rate at which drift and inbreeding alter genetic variance (Wright 1931). Populations with small N_e are more susceptible to the fixation of deleterious alleles and loss of additive adaptive variance, evolutionary changes that may lead to extirpation (Franklin 1980; Newman and Pilson 1997). There is no direct relationship between N_e and census size (N_c). The ratio of the two measures varies greatly, from 10^{-5} in many marine species to nearly 1.0 in some terrestrial vertebrates (Frankham 1995; Hedrick 2005), so N_e must be estimated from demographic and/or genetic data. Difficulty in obtaining the information required for demographic methods of estimating N_e has led to multiple formulations for estimating N_e from genetic data (Caballero 1994; Wang 2005).

There are two major categories of N_e estimates, contemporary N_e and historic N_e . While the latter has been examined in a conservation context by several authors (Roman and Palumbi 2003; Alter et al. 2007), it must be interpreted carefully as any past demographic change will have great affect on the estimate, making it hard to determine to what time period N_e applies (Crandall et al. 1999; Schwartz et al. 1999). This makes the results less informative for those interested in a current population's evolutionary potential. On the other hand, contemporary estimates of N_e apply to generations in the recent past and estimates of the effective number of breeders (N_b) apply directly to the parents of a sampled cohort (Waples 2005). Thus, these measures are more useful for proactive conservation and management.

In recent years, there has been increased interest in the incorporation of N_e estimates in fisheries management and

conservation (Ryman et al. 1995). In particular, there is concern that fishing may not only act as a selective agent (Law 2000), but may simultaneously reduce genetic variance (Jones et al. 2001; Hauser et al. 2002; Hutchinson et al. 2003). Estimation of contemporary N_e in this context has mostly relied on various versions of the temporal method, which estimates N_e from the variance in allele frequencies between two samples separated in time. To produce accurate estimates these methods generally require samples at least one generation apart (Waples 1989; Williamson and Slatkin 1999; Wang 2001). This method has been widely used in bony fishes (Hauser et al. 2002; Hutchinson et al. 2003; Hoarau et al. 2005; Poulsen et al. 2006) via archived scales or otoliths collected for aging studies. To date, there has not been an assessment of contemporary N_e for any shark species. This may be in part due to the lack of archived materials, as shark scales are not used in aging studies, but also because shark fisheries have generally existed over periods of time that are short relative to the target species' generation times (Anderson 1990; Hoff and Musick 1990). Thus estimation of N_e in elasmobranchs necessitates either methods that require a single sample (Waples 1991) or modified temporal estimators (Jorde and Ryman 1995).

Estimating current N_e for elasmobranchs is important because many species are fully exploited or overexploited in fisheries throughout the world's oceans and historically have not fared well under fishing pressure (Musick et al. 2000). In addition, elasmobranchs share some life history characteristics with mammals, such as slow growth, late maturity, internal gestation and low fecundity (Walker 1998; Stevens et al. 2000) and some with bony fishes, such as high dispersal potential. Understanding where the N_b/N_e of sandbar sharks falls in relation to terrestrial vertebrates and marine fishes may provide insight into the impact that exploitation has on genetic variance in elasmobranchs.

The sandbar shark, *Carcharhinus plumbeus*, is a heavily exploited species throughout most of its discontinuous global range. The species reaches maturity slowly and has low lifetime fecundity (Sminkey and Musick 1996), making it vulnerable to over-exploitation. The western North Atlantic population encompasses animals caught from Cape Cod all the way to the Gulf of Mexico (Heist et al. 1995). In the U.S. the sandbar shark comprises more than 2/3 of the directed commercial shark fishery (Castro 1993), and the stock has been in decline since the inception of the fishery (Musick et al. 1993). Mating occurs off the Atlantic coast of Florida and females, who bear live young, make long migrations every other year in the summer to inshore nursery grounds to give birth (Springer 1960). Nursery grounds are vital to the species as they provide an abundant supply of food for the growing pups and safety from large elasmobranch predators

found in greater number to the south (Springer 1960; 7Medved et al. 1985). Juveniles move offshore in the winter months but return to their natal nursery every summer for the first 4–12 years of life (Grubbs et al. 2007; McCandless et al. 2007)

The most important western North Atlantic nursery grounds are thought to be in the mid-Atlantic and include the lower Chesapeake Bay, the lagoons of the Eastern Shore of Virginia, and Delaware Bay (Grubbs and Musick 2007; McCandless et al. 2007). Therefore, estimating N_b and N_e in the Delaware Bay (DEL) and Eastern Shore lagoons (ES) may provide critical information about the long-term sustainability of the Atlantic stock. While temporally spaced samples are not available for such an estimate, as generation time is around 20 years, sampling in the summer allows for the collection of samples from discrete cohorts. This allowed us to estimate N_b and N_e using the linkage disequilibrium method (Hill 1981; Waples 1991, 2006) as well as a modified temporal method (Jorde and Ryman 1995) in two of the vital nursery areas and compare the values with estimates of N_e .

Materials and methods

Collection and genotyping

Juvenile sharks were captured from lagoons on the Eastern Shore of Virginia and from within the Delaware Bay between May and September 2003–2006 using research longline and gillnet gear as described by Branstetter and Musick (1993) and McCandless et al. (2007). Total length, fork length and standard length (length from tip of the snout to just before the caudal fin) were measured for each fish. A small piece of tissue was excised from the trailing portion of the first or second dorsal fin and animals were released. All animals were simultaneously tagged, ensuring that individuals were not resampled. Tissue was stored in 10% DMSO buffer (Seutin et al. 1991) at 4°C until extraction.

Since sandbar sharks exhibit placental viviparity, newborns have the remnants of the umbilicus and young-of-the-year (YOY) animals retain obvious umbilical scarring throughout the first months after birth. Therefore, individuals with open or recently healed birth scars were considered to be YOY. Since juveniles return to their natal nursery grounds, older individuals were used to augment cohorts where there were few YOY samples. Given that juvenile sharks were captured in this study at the time of the year when growth is greatest (Grubbs et al. 2007), length at age regressions lacked accuracy, so modal progression analysis following the methodology of Bhattacharya (1967) was implemented in FiSAT II (Gayanilo et al. 2005) to determine the age of older animals or those with late stage birth

scars. To place individuals into cohorts conservatively, only individuals within 2.0 standard deviations of the mean size for an age class were retained. In later months, when the distributions show greater overlap as variance in growth rate increases, only individuals within 1.5 standard deviations of the mean size for an age class were retained.

DNA was extracted using a modified Chelex extraction protocol (Estoup et al. 1996). A total of 902 juvenile sandbar sharks was genotyped at eight microsatellite loci. Markers were amplified for each individual using IR-700 and IRD-800 labelled forward primers. Descriptions of primers and PCR conditions for the six species-specific markers, Cpl153, Cpl190, Cpl128, Cpl132, Cpl166, Cpl169 are reported elsewhere (Portnoy et al. 2006, 2007). Two additional markers, Cli12 and Cli103, originally isolated from the congeneric blacktip shark, *Carcharhinus limbatus*, were surveyed following the protocols outlined in Keeney and Heist (2003). All amplicons were electrophoresed through 25 cm 6.5% polyacrylamide gels using a LiCor 4200 Global IR² system. A 50–350 bp size standard was run in the first, middle, and last lanes of each gel and locus-specific standards were run in every 4th lane. Alleles were scored manually with the aid of Gene ImagIR 4.05 (Scanalytics, Rockville MD). Twenty-five percent of samples were randomly selected and rescored to ensure accurate scoring. Individuals for which more than two loci could not be reproducibly scored were discarded.

Genetic data analysis

Conformance to the expectations of Hardy–Weinberg equilibrium was calculated in GENEPOP (Raymond & Rousset 1995) for each locus using 93–96 adult individuals selected to be representative of the species throughout its range in the western North Atlantic and Gulf of Mexico. Significance was assessed using exact tests with 10,000 iterations (Guo and Thompson 1992). Number of alleles and allelic diversity were calculated for each locus for the combined data set of juvenile samples using FSTAT (Goudet 2001). Micro-Checker (van Oosterhout et al. 2004) was used to screen for null alleles and genotyping errors. N_b and N_e were calculated using the linkage disequilibrium method in the program LDNe (Waples and Do 2008). This methodology calculates the correlation among alleles at unlinked loci (r), which can be related to N_e by the formula $N_e = \frac{1}{3*(r^2 - \frac{1}{S})}$ (Hill 1981; Waples 1991), where S is sample size. To correct for downward bias associated with small sample sizes, LDNe uses a modified version of this equation (Waples 2006). The data were analyzed keeping cohorts within nurseries separate, which estimates N_b for species with overlapping generations as long as yearly N_b does not fluctuate extensively (Waples 2005). The data were also examined

with all cohorts combined within nurseries to form an estimate that approximates generational N_e (Waples personal communication). Analyses were run sequentially excluding minor alleles at the 0.01, 0.02 and 0.05 frequency levels.

N_e was also estimated for ES and DEL samples using a modified temporal method (Jorde and Ryman 1995). This method examines shifts in allele frequencies between consecutive cohorts and relates them to N_e by the formula $N_e = \frac{C}{2GF_k}$, where G is generation time, F_k' is Pollack's F -statistic averaged across cohorts, and C is a parameter used to account for the probability of survival to age (l_i) and reproductive output of each age class (b_i). F_k was calculated between consecutive cohorts, sequentially excluding minor alleles at the 0.01, 0.02 and 0.05 frequency levels using SalmonNb (Waples et al. 2007), corrected for sample size and then averaged. In addition F_s , which is less biased by rare alleles than F_k , was calculated using TempoFs (Jorde and Ryman 2007) and used to estimate N_e . In order to estimate C and G , values of l_i were calculated using mean age-specific survivorships averaged across 10 different methods of estimation (Cortes and Brooks 2005). Given that there is no detectable relationship between female size and reproductive output in sandbar sharks and males are not sperm limited (Portnoy et al. 2007), b_i was calculated from the proportion of mature individuals in each age class using two maturity ogives which differ in the estimate of first maturity (Merson 1998; Romine unpublished data) to explore the effect that this parameter might have on estimates of N_e . G and C were calculated on a [©]Windows executable program (P. Jorde, personal communication). Confidence intervals were calculated assuming that the F -statistic is chi-square distributed (Waples 1989; Jorde and Ryman 1996).

Census estimates were generated for DEL 2004, 2005 and 2006. Briefly, the number of YOY sharks in the estuary (McCandless unpublished data) was divided by 8.4, the average yearly reproductive success of females (Sminkey and Musick 1996), to arrive at an estimate of the number of mature females. To estimate N_e (in this case the census number of breeders) the estimated number of females was then multiplied by 3.3, to account for the average number of sires per litter (2.3, Portnoy et al. 2007) or by 3 to account for the yearly operational adult sex ratio, which is 2:1 (M:F) because females reproduce once every two years while males reproduce annually (Springer 1960). Estimates of N_e excluding alleles at frequencies less than 0.02 were then compared with N_e . This criterion for excluding rare alleles was selected because it is sufficiently conservative to reduce upward bias in estimations of N_b created by rare alleles, without sacrificing too much of the precision provided by highly polymorphic loci (R. Waples personal

communication). For this reason, all results refer to the 0.02 exclusion category unless otherwise specified.

Results

The number of alleles per locus varied from 6 at Cpl53 to 74 at Cpl166. The genotypic distribution of all loci conformed to the expectations of Hardy–Weinberg equilibrium. No evidence of null alleles or scoring error due to stutter-bands was detected at any locus using the Micro-Checker software. All summary statistics, as well as expected and observed numbers of heterozygotes, are available in electronic Appendix A.

The linkage disequilibrium method returned fairly consistent estimates of N_b within nurseries across years. For most years, at least one estimate had confidence intervals that did not include infinity and estimates were often consistent across exclusion categories (0.01, 0.02 and 0.05, Table 1). For the most part, estimates of N_b were smaller with higher exclusion frequencies and larger with lower

exclusion frequencies (Table 1). Yearly estimates of N_b were larger in Delaware Bay than in the Eastern Shore lagoons (Table 1), with harmonic means of 1059 and 511, respectively. When the data across years within nursery grounds were combined and treated as a single sample, the linkage disequilibrium estimate of N_e was 4890 (1771– ∞ at 95% CI) for DEL and 2709 (1452–13,793 at 95 % CI) for ES (Table 2).

Generation time was calculated at 20.88 years when the Merson (1998) ogive was used and 19.04 when the Romine ogive (J. Romine personal communication) was used. C parameter estimates were 69.549 and 71.509 respectively, and both stabilized after about 100 generations (life history tables used to calculate G and C are available as electronic Appendix B). Though both sets of parameters gave similar N_e estimates, those using the Romine ogive were consistently larger (Table 2) and will be considered in the following results and discussion. Estimates of N_e using the Jorde and Ryman method for ES were consistent when minor alleles were excluded at the 0.01 and 0.02 levels and when F_s was used: 1619 (1326–1938 at 95% CI), 1409

Table 1 Yearly estimates of effective number of breeders (N_b) using the linkage disequilibrium method for the lagoons of the Eastern Shore of Virginia (ES) and Delaware Bay (DEL)

cohort	S	<0.01	<0.02	<0.05	N_c 2:1	N_c 2.3:1	N_b/N_c
ES2002	77	3751 (567– ∞)	427 (202– ∞)	184 (94–920)	NA	NA	NA
ES2003	139	1526 (684– ∞)	734 (404–3036)	886 (257– ∞)	NA	NA	NA
ES2004	99	922 (447– ∞)	469 (267–1560)	220 (111–1209)	NA	NA	NA
ES2005	106	1785 (556– ∞)	416 (234–1430)	227 (121–871)	NA	NA	NA
ES2006	85	776 (380–50295)	798 (314– ∞)	276 (115– ∞)	NA	NA	NA
DEL2004	142	1128 (591–8051)	1038 (488– ∞)	∞	2081	2289	0.50 (0.45)
DEL2005	201	1797 (878–154839)	1079 (585–4985)	701 (293– ∞)	2145	2360	0.50 (0.46)
DEL2006	53	3458 (344– ∞)	∞	1000 (113– ∞)	1598	1758	0.63 (0.57)

Estimates were made excluding alleles with frequencies less than 0.01, 0.02 and 0.05. N_b/N_c was calculated for DEL using two different census size estimates based on different operational sex ratios, N_c 2:1 (N_c 2.3:1). N_b values used in the ratio were at the <0.02 level except for DEL2006 which was at the <0.05 level. 95% confidence intervals are in parenthesis next to point estimate, sample size is S

Table 2 Estimates of effective size (N_e) for lagoons of the Eastern Shore of Virginia (ES) and Delaware Bay (DEL) using the linkage disequilibrium method (LD) and the Jorde and Ryman temporal method (JR)

	S	<0.01	<0.02	<0.05	F_s	N_c 2:1	N_c 2.3:1	N_e/N_c
ES(LD)	506	3003 (1763–8983)	2709 (1452–13793)	1530 (669– ∞)	NA	NA	NA	NA
DEL (LD)	396	3977 (1900– ∞)	4890 (1771– ∞)	3259 (761– ∞)	NA	5824	6406	0.84 (0.76)
ES(JR)Merson	506	1436 (1176–1719)	1249 (1022–1497)	3507 (2897–4176)	1231 (1031–1470)	NA	NA	NA
DEL (JR)Merson	396	2639 (2202–3114)	∞	1044 (854–1253)	951 (774–1146)	1908	2098	0.50 (0.45)
ES(JR)Romine	506	1619 (1326–1938)	1409 (1153–1687)	3954 (3266–4708)	1266 (1041–1511)	NA	NA	NA
DEL(JR)Romine	396	2975 (2481–3509)	∞	1177 (962–1412)	978 (796–1177)	1908	2098	0.51 (0.47)

Estimates were made excluding alleles with frequencies less than 0.01, 0.02 and 0.05. Demographic parameters for JR were taken from one of two maturity ogives Romine (unpublished data) or Merson (1998). N_e/N_c was calculated for DEL using two different census size estimates based on different operational sex ratios, N_c 2:1 and N_c 2.3:1. N_e values used in the ratio were calculated using F_s . 95% confidence intervals are in parenthesis next to point estimate, sample size is S

(1153–1687 at 95% CI) and 1266 (1041–1511 at 95% CI), respectively. However, when alleles less frequent than 0.05 were excluded, the estimate was somewhat larger; 3954 (3266–4708). Estimates of N_e for DEL were larger at the 0.01 level than both the estimate at the 0.05 level and the estimate using F_s : 2975 (2481–3509), 1177 (962–1412) and 978 (796–1177) respectively. At the 0.02 level the estimate was infinity because sampling error was too great compared to F_k between 2005 and 2006.

The census number of YOY sharks in Delaware Bay was estimated at 5826 in 2004, 6006 in 2005, and 4474 in 2006 (McCandless unpublished data). This corresponds to approximately 693, 715, and 533 mature breeding females, an N_e of breeders of 2289, 2360 and 1758 when patterns of polyandry are taken into account (2.3:1) or 2081, 2145 and 1598 when only the operational sex ratio is accounted for (2:1). N_b/N_e was 0.45 or 0.50 in 2004, 0.46 or 0.50 in 2005 and 0.57 or 0.63 in 2006, respectively (Table 1). Using the linkage disequilibrium method over the three year period, the estimated N_e/N_c was 0.76 or 0.84 at the 0.02 level. The smallest N_e estimate using this methodology, at the 0.05 level, yielded ratios of 0.51 or 0.56. Using the Jorde and Ryman temporal method the estimated N_e/N_c was 0.55 or 0.60 at 0.05 level and was 0.47 or 0.51 when F_s was used but was greater than one at the 0.01 level (Table 2).

Discussion

Using both the linkage disequilibrium and Jorde and Ryman temporal methods, with reasonable sample sizes, we were able to obtain robust estimates of both N_e and N_b that differed from infinity, even though some estimates were in the thousands. This is a very encouraging result for the use of genetic methods for estimating N_e , as these methods work best when N_e is small but may have difficulty in distinguishing larger N_e from infinity. This study has demonstrated that with appropriate sample sizes and sampling design, these approaches are useful not only for conservation and management of shark species but also for other animals whose true N_e is greater than a few hundred.

Our estimates varied slightly between methods and exclusion categories, but were of the same magnitude. Estimates of N_b for DEL 06 using the linkage disequilibrium method and N_e for DEL using the Jorde and Ryman method at the 0.02 level were infinite because the larger error associated with the smaller 2006 sample size likely obscured the weak drift signal associated with larger true N_b or N_e . For the remainder of the samples the methodology worked well with reasonable sampling effort ($N = 77$ –139). A concern was that if animals stray from their natal nursery, the inclusion of animals collected up to

two years after birth might affect estimates. Yet the ES02 estimate, which was composed entirely of tissues collected in 2003 and 2004, was consistent with all other years. In fact, if juvenile straying had been present, one would expect the estimate of N_b to be larger for that year; however, it was the second smallest estimate. In addition, because generation time (20 years) is much longer than the sampling interval (3–5 years), care had to be taken when interpreting N_e estimates calculated using the linkage disequilibrium method for pooled cohorts. In this study, the validity of this estimate is supported by two facts. First parents across all age classes are likely represented in each cohort and second estimates of N_e calculated using this methodology were consistently larger than the estimates of N_b . Since parturition occurs only once in a given year, estimates within the same year at the different nurseries should be considered independent. Caution should be taken in summing these estimates within a year across sampling locations to get cumulative reproductive effort estimates because males are likely represented in progeny found in both locales.

The estimated N_b/N_c and N_e/N_c in sandbar sharks were close to 0.5, which conforms to expectations for random mating populations with overlapping generations (Nunney 1993). It is important to note that comparisons of N_e/N_c across studies must be made with caution, not only because differing methodologies define and calculate N_e differently, but because the appropriate definition of N_e will differ as well (Nunney and Elam 1994). In this study for example, N_e estimated using the Jorde and Ryman temporal methods applies to an entire generation and because females breed only every other year, N_e and N_c are harmonic means across years (Waples 1991), whereas the linkage disequilibrium method N_e applies directly to the breeders that generated the given sample (Waples 2005). This explains in part why N_e estimates made using the Jorde and Ryman temporal method are smaller than those made using the linkage disequilibrium method. Finally, care must be taken with comparisons between species because as N_e decreases, variance in reproductive success may decrease causing an increase in N_e/N_c (Ardren and Kapuscinski 2003). Nonetheless, our estimates of N_e/N_c were similar across methodologies and the smallest ratio obtained in this study was 0.45. If the outer estimates of the confidence intervals obtained for N_e are used to calculate N_e/N_c , the ratio falls between 0.21–1.0, which is higher than the average for wildlife reported by Frankham (0.10–0.11, 1995) and orders of magnitude larger than most marine species examined (10^{-3} – 10^{-5} , Hoarau et al. 2005). Finally, while different methodologies can result in different N_e/N_c ratios, it is unlikely that bias alone could explain such large differences in ratios between this study and those examining other marine fishes.

The relatively high estimated N_e/N_c in sandbar sharks is much closer to values reported for mammals than for marine fishes (Fig. 1). Variation of family size, unequal contribution of males and females, and non-random mating are all factors that cause N_e to be lower than N_c (Falconer and Mackay 1996). In marine species, which are typically highly fecund, the low ratio has been attributed to large variance in reproductive success (Hedgcock 1994). Female sandbar sharks invest heavily in decreasing offspring mortality through long gestation periods and migrations to nursery grounds (Branstetter 1990), and there is low variance in female fecundity (Sminkey and Musick 1996). In addition, an even sex ratio (Springer 1960) and aggressive male mating tactics that may make female mate choice difficult (Pratt and Carrier 2001; Portnoy et al. 2007) are factors that could maintain N_e close to N_c . Many of these characteristics are shared by other shark species and some, such as increased parental investment and increased offspring survival, are present in mammals.

Populations with N_e smaller than 500 are thought to be at risk of losing genetic variation via drift (Franklin and Frankham 1998). Our estimates of N_b were on the order of 400–1000 and N_e estimates made across years were at least twice as large (1408–4890). However, there is evidence

that the N_e needed for a population to retain evolutionary potential may be as large as 5000 (Nunney and Campbell 1993; Lande 1995). Even so, our estimates apply only to the nursery grounds where sampling took place, so it is not likely that the species in western North Atlantic is at risk of losing adaptive genetic variance. The close coupling of N_e and N_c reported in this study, despite heavy exploitation, also means that as long as N_c is maintained well above 10,000, the species' evolutionary potential should not be compromised.

The possibility that N_e and N_c are closely coupled in other elasmobranch species may be cause for concern given the fully exploited or overexploited status of many of these species (Musick et al. 2000). Marine species with low N_e/N_c ratios tend to feature high fecundity and/or population growth rates which give them the potential to maintain genetic diversity and/or avoid the fixation of deleterious alleles despite large fluctuations in N_c (Lesica and Allendorf 1992; Mills and Smouse 1994; Lynch et al. 1995). Evidence that populations may be maintained over long periods of varying N_e with stable N_e exists for bony fishes (Grant and Bowen 1998; Ruzzante et al. 2001; Poulsen et al. 2006). For shark species, where N_e/N_c is high and rebound potential is low (Smith et al. 1998), continued

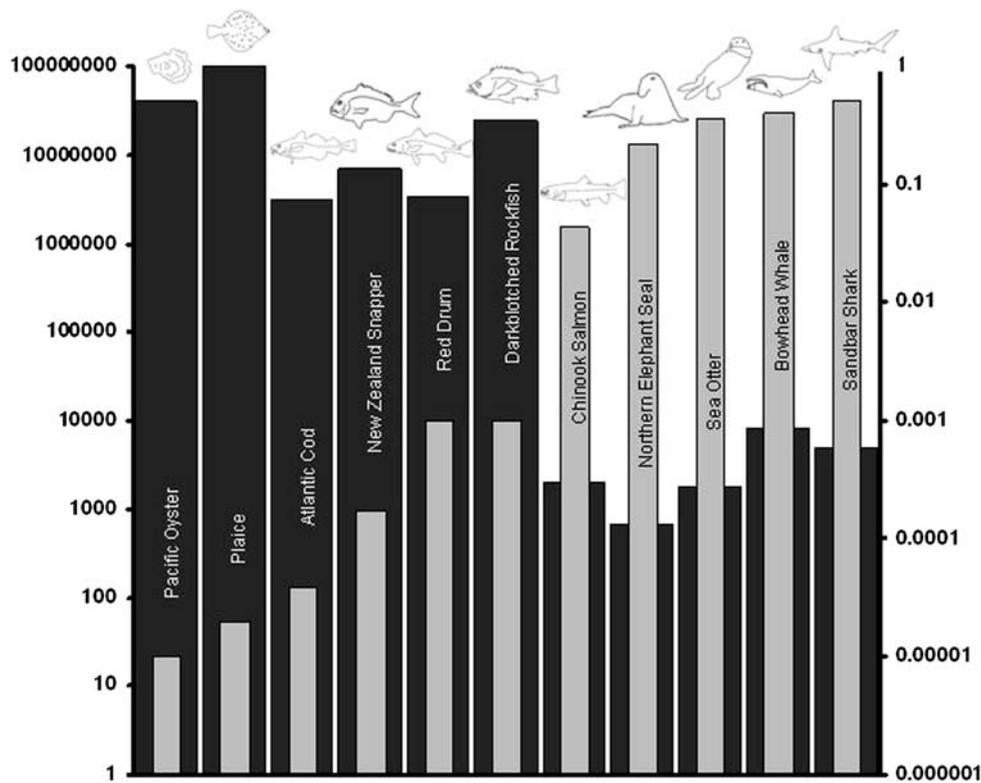


Fig. 1 Ratio of effective size to census size (N_e/N_c) and census size (N_c) estimated for wild populations of marine and anadromous species of management and conservation interest (both axes in log-scale). Forward bars are N_e/N_c (right axis), back set bars are N_c (left axis).

Estimates were taken from the literature (Ralls et al. 1983; Bartley et al. 1992; Nunney 1993; Hedgcock 1994; Shelden et al. 2001; Turner et al. 2002; Hauser et al. 2002; Hutchinson et al. 2003; Hoarau et al. 2005; Gomez-Uchida and Banks 2006)

removal of biomass may result in the erosion of genetic variance with no means of compensation. While loss of additive genetic variance may not immediately affect fitness, such decreases may leave populations unable to adapt to ecological change, increasing the probability of localized extirpation.

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