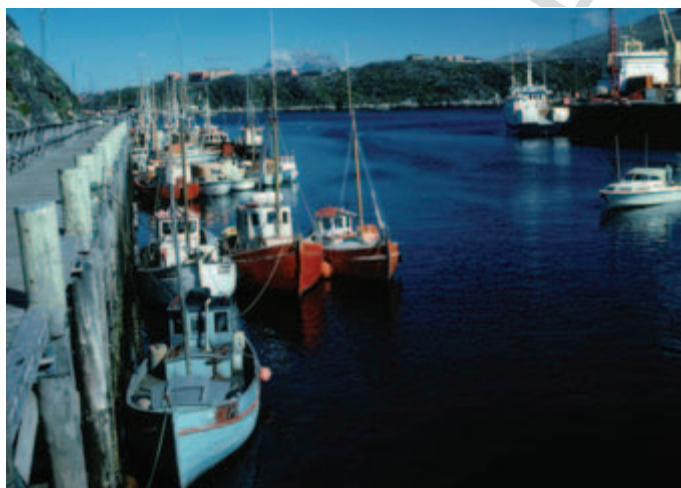# 10
Fisheries Exploitation

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Upper: boats involved in the high seas fishery for Atlantic salmon off the West Greenland coast, in Nuuk harbour, Greenland, 1986. Lower: spring angling for salmon on the River Corrib, Galway, Ireland using spinners and fly. (Photos credit: E. Verspoor.)

The exploitation of Atlantic salmon, *Salmo salar*, in food and recreational fisheries has a long history in the rivers and coastal waters of the species range. Fortunately, prior to the last few centuries, when river stocks were largely healthy, exploitation was not a serious management concern. However, increasingly with many populations in decline, fisheries exploitation has come to be a major concern for managers of salmon fisheries, both in rivers and in the sea. Until recently, most of this concern focused on the direct threat posed by the reduction in numbers. However, recent research suggests that the impacts are likely to be more complex and insidious through effects on the genetic structure of the affected populations.

10.1 Introduction

The Atlantic salmon is a highly sought-after species, and has probably been so since humans colonised the Atlantic coasts of Europe and North America many thousands of years ago. Atlantic salmon can be found as 40 000-year-old bone remains in Spanish caves (Consuegra *et al.* 2002), and as 6000 to 10 000-year-old rock paintings and rock carvings in Norway and Sweden (Fig. 10.1). Moreover, the species is one among very few that are mentioned in the earliest national legislation (e.g. from the thirteenth century in Norway), and its exploitation is continually a matter of strong national and international regulation (NASCO 2005). The species is exploited for food and recreation, both with strong economic implications. This generates potential conflicts not only among nations, but also between commercial and recreational interests within nations. The high value of Atlantic salmon as a resource invites overexploitation, which has led to concerns about population viability and evolutionary change in exploited populations (Schaffer and Elson 1975).

Exploitation can have evolutionary consequences. One is the selective removal of highly valued species, often large-sized and late-maturing top predators (Atlantic salmon being one of them), followed by successive concentration on smaller species, often at lower trophic levels (Pauly *et al.* 1998). Other effects of exploitation include selection of particular populations within species and selection of particular phenotypes within populations, both of which may have genetic consequences. Selective removal of populations can occur even if the fishery itself is nonselective. When fishing mortality is high and several populations contribute to the fishery, differences in life history and productivity may lead to the less productive populations being selectively removed (Larkin 1977). Finally, undirected (random) loss of genetic variation within populations occurs when exploitation reduces spawning escapement and subsequently

Fig. 10.1   Rock paintings of salmonids from Tingvoll, Norway, 6000 years BP. Actual size is ~ 1 m body length. (Image credit: K. Hindar.)

the effective population size of the population (Wright 1969). All types of genetic effects (selection among and within populations, and increased genetic drift) can be viewed as loss of genetic variation. The topic has previously been reviewed by Miller (1957) who did not find evidence of genetic change caused by selective fishing, and more recently by Nelson and Soulé (1987) and Thorpe (1993) who found some evidence of genetic effects caused by fishery exploitation. Recently, genetic changes in life-history traits caused by selective fishing have been implicated in the collapse of the northern cod, *Gadus morhua*, off Labrador and Newfoundland (Olsen *et al.* 2004).

The number of wild Atlantic salmon may now be at an all-time low (Kellogg 1999; Crozier *et al.* 2003). Small population sizes may lead to increased rates of inbreeding and loss of genetic variation, which may in turn have direct negative consequences for a number of fitness-related traits (Nelson and Soulé 1987; Chapter 8). Moreover, loss of genetic variation can reduce the potential for a population to adapt to changing environments (Lande and Shannon 1996; Chapter 7). Indeed, the genetically effective size of a population has been used as one criterion for determining the extinction risk, e.g. in the World Conservation Union (IUCN) guidelines for categorising threatened species (Mace and Lande 1991).

In fisheries management, consideration of the effective population size translates into finding conservation limits that set constraints on the maximum yield that can be sustainably harvested from the populations. A problem, however, is that conservation guidelines have been designed for isolated populations, whereas anadromous salmon populations – although genetically different – are only partially isolated from one another (Ståhl 1987; Chapter 5). This means that the level of genetic variation is a function not only of the population size and demography of the local population, but also of the neighbouring populations and of the level of migration (gene flow) among them. A few migrants between populations can provide input to reduce the risk of inbreeding and loss of genetic variation even though they do not contribute much to reduce demographic risks in a local population (Waples 1998).

In this chapter, we present fisheries exploitation in a biological and management context, review harvest rates of Atlantic salmon populations, outline possible genetic effects of fishing, and examine the evidence for genetic changes caused by fishing of Atlantic salmon.

10.2 A historical perspective on fisheries exploitation

The exploitation of Atlantic salmon in fresh water constitutes probably the oldest kind of fishery (Cleyet-Merle 1990). Spears and fixed engines have been used in a number of rivers, especially where salmon had to pass through rapids and other narrow parts. In wider and more slow-flowing rivers, seines and other nets have been more common. Today, most of the freshwater catch of Atlantic salmon is by rod and line (Fig. 10.2), a tradition that was brought by Britons to most of the world's salmon-producing rivers in the nineteenth century and which has reached high popularity throughout the range of the species.

Along the coasts, bag nets (Fig. 10.3), bend nets and other fixed engine methods have century-old traditions. These methods developed in areas where the migratory routes of salmon from many rivers coincide, and can be highly efficient in narrow fjords and in other locations where migrating salmon seek near shore. In the open ocean, exploitation of Atlantic salmon took place from the late 1950s. The methods used were drift nets and long-line fishing operated from ocean-going vessels.

Fig. 10.2 Rod-caught Atlantic salmon from the River Verdalselva, Norway. (Photo credit: D.H. Karlsen.)

Fig. 10.3 Bag net in the Drammensfjorden, Norway. (Photo credit: L.P. Hansen, NINA.)

Concerns about the decline of salmon populations from the 1980s, and the mixed-stock nature of fishing in the ocean, led to strong regulations of both coastal and oceanic fisheries. Quotas for the fisheries around the Faroes and off West Greenland have since 1984 been set by an international body (North Atlantic Salmon Conservation Organization, NASCO) based on scientific advice from the International Council for the Exploration of the Sea (ICES). Although Atlantic salmon use vast areas in the North Atlantic Ocean during their feed-ing migration, populations from different regions are concentrated in different oceanic areas. In the West Greenland fishery, salmon from North America (Canada, USA) are represented

along with European populations from Scotland, Ireland, the United Kingdom (UK) (excluding Scotland), France and Spain, whereas in the Faroes fishery, populations from Norway, Scotland, Russia, Ireland and the UK are represented (Crozier *et al.* 2003). Genetic methods (allozymes and DNA) can be used to distinguish between continental origins of salmon in the West Greenland fishery (Verspoor 1988; Chapter 5). Such a mixed-fishery analysis has been taken a step further in the Baltic Sea, where the relative contributions of all stock groups that are considered important from a fisheries management point of view are estimated on the basis of DNA microsatellite variation (Chapter 9; Koljonen *et al.* 2005).

Following the regulation of coastal and oceanic fisheries, in-river fisheries account for an increasing proportion of the salmon catches in the North Atlantic. In 2004, 66% of North American catches took place in rivers compared to 42% in north-east Atlantic countries (ICES 2005). Another trend is an increase in the use of catch and release by anglers. While Russia reported that 76% of the total rod catch was released during the 2004 angling season, this practice is viewed with scepticism by animal health authorities in Norway. They consider catch and release in numerically strong populations as being unethical, whereas selective release of wild salmon can be acceptable where a vulnerable population coexists with sea trout and/or escaped farm salmon that are targeted for capture (Statens Dyrehelsetilsyn 2002). Countries also differ widely in other types of fisheries regulation. However, a common pattern is that regulation is based on concepts of catch rate and/or spawning escapement.

10.2.1 Catch statistics

The reported catch of Atlantic salmon in the North Atlantic peaked at about 12 000 tonnes annually in 1973–75, and thereafter showed a steady decline to less than 2500 tonnes during the last few years (Fig. 10.4). In the peak years during the 1960s and 1970s, catches reached 2000 tonnes or more in several countries, including Canada, Norway, Ireland and the UK (Scotland, in particular). Recently, only the Norwegian catches have reached 1000 tonnes. The decline in total catch from the 1980s is partly explained by the closure or regulation of
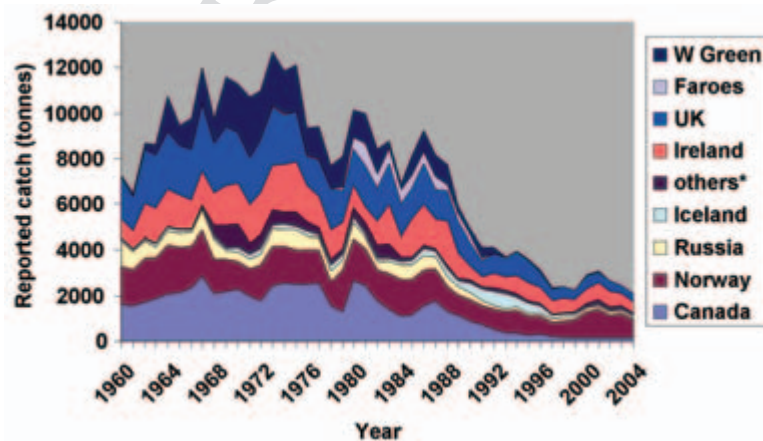

Fig. 10.4   Total reported catches 1960–2004 of Atlantic salmon in the North Atlantic, including river, coastal and oceanic fisheries. * = USA, Sweden, Denmark, Finland, France and Spain (1960–2004), and catches in the Norwegian Sea (1968–1984). Based on data from ICES (2005).

some fisheries, especially at sea. For example, the West Greenland fishery accounted for 2000 tonnes or more in the early 1970s (Fig. 10.4), but now accounts for less than 20 tonnes (ICES 2005). Likewise, the significance of the Faroes fishery, which reached 1025 tonnes in 1981, is now negligible. In the Norwegian Sea, two other fisheries peaked at around 1000 tonnes within this period: long-lining in 1970 (closed from 1984 onwards) and drift nets in 1981 (closed from 1989). However, the decline in catches also reflects lower survival rates of Atlantic salmon in the ocean (Friedland *et al.* 1998), and possibly reduced smolt production caused by habitat degradation (WWF 2001).

10.2.2 Exploitation rates

Estimates of exploitation rates on Atlantic salmon populations suggest that variable and sometimes high proportions of returning adults are caught in sea and river fisheries (Table 10.1a,b). The highest exploitation rates for rod and line are found in Norway, Iceland and Spain, where in-river exploitation rates often exceed 0.30. Salmon in rivers of the United Kingdom and Ireland typically experience lower rates of exploitation, but may in addition be exploited by net and coble used in the estuaries (e.g. Shearer 1992).

Exploitation rates can also be high in the marine environment (Table 10.1a,b). During the early 1980s, marine exploitation rates were estimated at 0.70 or above for many salmon populations on either side of the North Atlantic Ocean (Hansen 1988; Crozier and Kennedy 1993; Dempson *et al.* 2001), Iceland being a possible exception (Scarnecchia *et al.* 1989). The rise and fall of the Faroes and West Greenland fisheries (Fig. 10.4) suggest temporally variable exploitation rates of salmon in the sea, with a significant decline during recent years.

10.2.3 Potential for selection

River fishing is targeted on sexually maturing anadromous fish. Although the methods used may not directly select for body size, indirect selection may occur through selection on run timing which varies both within and between populations. A common pattern is that early-run, large fish are more heavily exploited than late-run, smaller fish (Gee and Milner 1980; Consuegra *et al.* 2005a). Consistent with this is that subpopulations spawning in the upper tributaries may be subject to higher exploitation rates than those spawning downstream (Youngson *et al.* 2003). An opposite pattern is seen in some Norwegian rivers, where 1-sea-winter (1SW) fish seem to be more heavily exploited than multi-sea-winter fish (Sættem 1995; Sandhaugen and Hansen 2001). An apparently nonselective river fishery is the net fishing on some Russian rivers, where the entire river is closed every second or third day. Another example may be catch-and-release fishing. Catch and release may impose little mortality on the fish, provided water temperatures are low, but may affect the behaviour after release (Dempson *et al.* 2002; Thorstad *et al.* 2003). At any rate, all fishing is likely to act more strongly on anadromous individuals than on individuals maturing in fresh water (Caswell *et al.* 1984).

Most fishing methods used in the marine environment are size-selective, especially as a particular mesh size of the nets catches fish with a certain girth size with higher probability than either larger or smaller fish. Also, the potential for selection is stronger in marine than in river fisheries, as both immature and maturing salmon may be targeted for capture. By being size-selective, these methods can also select among populations, for example by not catching populations that return as 1-sea-winter salmon to spawn.

Table 10.1a Exploitation rates sustained by different Atlantic salmon populations.

Population (Country)	Period	Environment	Type of fishery	Stock origin	Age class	Exploitation rate Mean	Range	Reference
North America								
Newfoundland								
Little Codroy River	—	Marine	Nets	W	1SW	0.47	—	Murray (1968)
	—	Marine	Nets	W	MSW	0.75	—	"
Western Arm Brook	—	Marine	Nets	W	1SW	0.62	—	Reddin (1981)
	—	Marine	Nets	W	1SW	0.65	—	Chadwick et al. (1985)
	1984–91	Marine	Nets	W	1SW	0.57	0.40–0.64[1]	Dempson et al. (2001)
	1984–91	Marine	Nets	W	MSW	0.96	0.94–0.99[1]	"
Exploits River	1984–91	Marine	Nets	W	1SW	0.46	0.24–0.62[1]	"
	1984–91	Marine	Nets	W	MSW	0.76	0.55–0.86[1]	"
Gander River	1984–91	Marine	Nets	W	1SW	0.66	0.66–0.70[1]	"
	1984–91	Marine	Nets	W	MSW	0.72	0.55–0.82[1]	"
Middle Brook	1984–91	Marine	Nets	W	1SW	0.37	0.22–0.49[1]	"
	1984–91	Marine	Nets	W	MSW	0.80	0.66–0.88[1]	"
Terra Nova River	1984–91	Marine	Nets	W	1SW	0.35	0.22–0.45[1]	"
	1984–91	Marine	Nets	W	MSW	0.69	0.60–0.78[1]	"
NE Placentia River	1984–91	Marine	Nets	W	1SW	0.39	0.20–0.53[1]	"
	1984–91	Marine	Nets	W	MSW	0.74	0.58–0.85[1]	"
	—	River	Rods	W	1SW+MSW	0.38	—	Chadwick (1982)
Humber River	1984–91	Marine	Nets	W	1SW	0.47	0.23–0.63[1]	Dempson et al. (2001)
	1984–91	Marine	Nets	W	MSW	0.60	0.34–0.72[1]	"
Lomond River	1984–91	Marine	Nets	W	1SW	0.28	0.12–0.41[1]	"
	1984–91	Marine	Nets	W	MSW	0.63	0.42–0.77[1]	"
Torrent River	1984–91	Marine	Nets	W	1SW	0.56	0.39–0.66[1]	"
	1984–91	Marine	Nets	W	MSW	0.75	0.57–0.86[1]	"
Middle Brook	1984–99	River	Rods	W?	1SW	0.26	0.06–0.53	O'Connell (2003)
Indian Bay Brook	1997–99	River	Rods	W?	1SW	0.14	0.12–0.16	"
Labrador								
Sand Hill River	—	Marine	Nets	W	1SW	0.33	—	Peet & Pratt (1972)
	—	Marine	Nets	W	1SW	0.36	—	Reddin (1981)
	—	Marine	Nets	W	MSW	0.90	—	Peet & Pratt (1972)
	—	Marine	Nets	W	MSW	0.92	—	Reddin (1981)

Location / River	Years	Habitat	Gear	Origin	Sea-age	Mean	Range	Reference
New Brunswick								
NW Miramichi River	—	Marine	Nets	W	1SW	0.32	—	Saunders (1969)
	—	Marine	Nets	W	1SW	0.34	—	Kerswill (1971)
	—	Marine	Nets	W	MSW	0.87	—	Saunders (1969)
	—	Marine	Nets	W	MSW	0.78	—	Kerswill (1971)
SW Miramichi River	—	Marine	Nets	W	1SW	0.36	—	"
	—	Marine	Nets	W	MSW	0.92	—	"
Salmon River	—	River	Rods	W	1SW+MSW	0.16	—	Chadwick (1982)
Nova Scotia								
Liscomb River	—	Marine	Nets	H	1SW	0.36	—	Semple & Cameron (1990)
	—	Marine	Nets	H	MSW	0.79	—	"
Maine								
Lakes		Lakes (landlocked)	Rods	H/W	—	—	0.18–0.41	Warner & Havey (1985)
Machias River	1962–72	River	Rods	H/W	1SW+MSW	0.20	0.12–0.22	Baum (1997)
Narraguagus River	1962–74	River	Rods	H/W	1SW+MSW	0.26	0.11–0.41	"
Penobscot River	1969–94	River	Rods	H/W	1SW+MSW	0.09	0.01–0.28	"
Europe								
Iceland								
R. Haukadalsá		Marine	Nets	W	MSW	0.16	—	Scarnecchia *et al.* (1989)
Laxá í Leirársveit		Marine	Nets	W	MSW	0.48	—	"
Laxá í Kjós		Marine	Nets	W	MSW	0.29	—	"
Thverá		Marine	Nets	W	MSW	0.21	—	"
Nordurá	—	Marine	Nets	W	MSW	0.28	—	"
	1972–85	River	Rods	W	1SW+MSW	0.25	0.11–0.82	"
Laxá í Dölum		Marine	Nets	W	MSW	0.27	—	Scarnecchia *et al.* (1989)
Fáskrúd		Marine	Nets	W	MSW	0.28	—	"
R. Ellidaár	1965–76	River	Rods	W	1SW+MSW	0.35	0.18–0.58	Gudjonsson (1988)
R. Úlfarsá	1955–63	River	Rods	W	1SW+MSW	0.29	0.14–0.46	"
R. Blandá	1982–85	River	Rods	W	1SW+MSW	0.65	0.55–0.82	"
avg of 3 rivers	—	River	Rods	W	1SW	—	0.39–0.73	Gudjonsson *et al.* (1996)
	—	River	Rods	W	MSW	—	0.75–0.84	"
Northern Ireland								
R. Bush	1983–90	Marine+coastal	Nets	H	1SW	0.77	0.46–0.94	Crozier & Kennedy (1993)
	1983–90	Marine+coastal	Nets	W	1SW	0.70	0.62–0.89	"
	1983–90	Marine+coastal	Nets	H/W	MSW	0.45	0.36–0.60	"
	1973–88	River	Rods	—	1SW+MSW	0.11	0.05–0.17	Crozier & Kennedy (2001)

Table 10.1a *(cont'd)*

Population (Country)	Period	Environment	Type of fishery	Stock origin	Age class	Exploitation rate Mean	Exploitation rate Range	Reference
R. Burrishoole	—	Marine+coastal	Nets	H	1SW	—	0.52–0.90	Crozier & Kennedy (1994)
	1970–80	River	Rods	H	1SW	0.11	0.03–0.24	Mills & Piggins (1983)
	1970–80	River	Rods	W	1SW	0.14	0.07–0.23	"
R. Erne	1970–81	River	Rods	W?	1SW+MSW	0.12	0.06–0.20	Mills *et al.* (1986)
	1970–81	Marine+coastal	Nets	H	1SW	0.12	0.54–0.64	Crozier & Kennedy (1994)
Scotland								
West coast	1981–83	Coastal	Nets	W	1SW	0.04	0.02–0.04[2]	Shearer (1992)
		Estuary	Nets	W	1SW	0.03	0.04–0.05[2]	"
		River	Rods	W	1SW	0.05	0.03–0.14[2]	"
North-west coast	1979–81	Coastal	Nets	W	1SW	0.06	0.06–0.08[2]	"
		Estuary	Nets	W	1SW	0.03	0.02–0.04[2]	"
		River	Rods	W	1SW	0.02	0.02–0.04[2]	"
North coast	1977–79	Coastal	Nets	W	1SW	0.06	0.05–0.07[2]	"
		Estuary	Nets	W	1SW	0.10	—	"
		River	Rods	W	1SW	0.03	0.03–0.04[2]	"
North-east coast	1985–88	Coastal	Nets	W	1SW	0.17	0.05–0.23[2]	"
		Estuary	Nets	W	1SW	0.02	0.00–0.03[2]	"
		River	Rods	W	1SW	0.05	0.03–0.08[2]	"
Moray Firth	1978–83	Coastal	Nets	W	1SW	0.11	0.07–0.15[2]	"
	1978–83	Estuary	Nets	W	1SW	0.09	0.04–0.15[2]	"
	1978–83	River	Rods	W	1SW	0.05	0.02–0.06[2]	"
	1983	Coastal	Nets	W	MSW	0.08	0.04–0.12[2,3]	"
	1983	Estuary	Nets	W	MSW	0.06	0.03–0.09[2,3]	"
	1983	River	Rods	W	MSW	0.04	—	"
East coast	1954–78	Coastal	Nets	W	1SW	0.29	0.23–0.37[2]	"
	1954–78	Estuary	Nets	W	1SW	0.26	0.19–0.35[2]	"
	1954–78	River	Rods	W	1SW	0.01	0.01–0.02[2]	"
	1952–78	Coastal	Nets	W	MSW	0.27	0.24–0.32[2]	"
	1952–78	Estuary	Nets	W	MSW	0.28	0.16–0.36[2]	"
	1952–78	River	Rods	W	MSW	0.04	0.04–0.08[2]	"
R. North Esk	1981–87	Estuary	Nets	W	1SW	0.27	0.15–0.40	"
	1981–87	Estuary	Nets	W	MSW	0.40	0.29–0.59	"
	1981–91	Sea (Faroes)	L.Line	W	1SW	—	0.00–0.04	MAFF/SOEFD/WOAD (1999)
	1981–91	Sea (Faroes)	L.Line	W	MSW	—	0.00–0.18	"

River	Year	Location	Gear	W/H	Sea age	Value	Range	Reference
R. Spey	1983–85	Estuary	Nets	W	1SW+MSW	0.09	0.04–0.11[2]	Shearer (1988)
R. Spey	1983–85	River	Rods	W	1SW+MSW	0.06	0.05–0.08	"
Wales								
R. Wye	1925–34	River	Rods	W	1SW+MSW	0.25	—	Gee & Milner (1980)
R. Wye	1965–74	River	Rods	W	1SW+MSW	0.47	—	"
Norway								
R. Imsa	1981–84	Marine+coastal	Nets	H	1SW	0.88	0.82–0.96	Hansen (1988)
R. Imsa	1981–84	Marine+coastal	Nets	W	1SW	0.77	0.66–0.84	"
R. Imsa	1981–84	Marine+coastal	Nets	H	MSW	0.97	0.94–1.00	"
R. Imsa	1981–84	Marine+coastal	Nets	W	MSW	0.94	0.94–0.95	"
R. Drammenselv	—	Marine+coastal	Nets	H	1SW	—	0.37–0.81	"
	—	Marine+coastal	Nets	H	MSW	—	0.22–0.70	"
	—	River	Rods	H	1SW+MSW	0.33	—	Hansen et al. (1986)
	—	(downstream)	Rods	H	1SW+MSW	0.04	—	"
	1985–90	River (upstream)	Rods	H	1SW+MSW	—	0.33–0.53	Hansen (1990)
		River						
R. Lærdalselv	1960–74	River	Rods	W	1SW+MSW	0.54	0.44–0.61	Jensen (1981)
R. Eira	1966–74	River	Rods	W	1SW+MSW	—	0.46–0.83	"
Finland								
R. Tana	1995	River	Nets	W	1SW	0.51	—	Karppinen et al. (2004)
R. Tana	1995	River	Rods	W	1SW	0.21	—	"
	1992–93	River	Nets	W	MSW	0.27	0.27–0.28	Erkinaro et al. (1999)
	1992–93	River	Rods	W	MSW	0.27	0.13–0.41	"
Spain								
R. Bidasoa	1980–2000	River	Rods	H/W	1SW+MSW	0.25	0.08–0.53	Alvarez & Lamuela (2001)
R. Bidasoa	1992–2000	River	Rods	H/W	1SW	0.10	0.06–0.14	"
R. Bidasoa	1992–2000	River	Rods	H/W	MSW	0.29	0.07–0.45	"
R. Nansa	1986–95	River	Rods	W	1SW+MSW	0.21	0.12–0.36	García de Leániz et al. (1992, unpbl)
R. Asón	1982–96	River	Rods	W	1SW+MSW	0.40	0.17–0.64	"

[1] 5th–95th percentiles.
[2] Exploitation of vulnerable population available to the fishery (rather than total population).
[3] 95% CL.

Table 10.1b Summary of differential exploitation ratios calculated from paired comparisons in Table 10.1a.

Character examined in paired comparisons of exploitation rates	Mean ratio of differential exploitation	Range	No. of studies (*n*)
(a) By fishery (nets/rods	3.05	1.00–5.33	9
(b) By age class (MSW/1SW)			
in rod fisheries	2.25	0.80–4.00	4
in net fisheries	1.65	0.53–2.73	24
(c) By stock origin (wild/hatchery)	1.04	0.88–1.27	3

10.3 Fisheries exploitation as an ecological and evolutionary force

Fishing affects the biomass of most of the world's major fish resources, with large ecosystem effects through fishing down marine food webs (Pauly *et al.* 1998). During recent decades, several of the world's major fisheries have shown significant collapses, and in 1997, the Food and Agriculture Organization (FAO) estimated that 60% of the major marine fisheries were either fully exploited or overexploited, some of them even to the point where they would be designated 'vulnerable' by the threat categories of IUCN (1999). The recovery of overexploited populations is not necessarily as rapid as was generally believed for high-fecundity species (Hutchings 2001), and it is possible to exploit salmon populations to extinction. In common stock-recruitment (SR) models, this occurs when the exploitation rate exceeds the maximum reproductive rate of the population, which is determined by the slope of the stock-recruitment curve near the origin. Estimates of this slope (R/S near the origin) in salmonid fishes suggest that maximum sustained exploitation rates are between about 65 and 80% (Potter *et al.* 2003). With small numbers of spawners, however, other factors such as local inbreeding depression (Lynch 1991) and local demographic and environmental stochasticity (Lande *et al.* 1999) need to be taken into consideration, as they may reduce the reproductive capacity below what is inferred from deterministic SR models.

Here we are concerned with two types of loss of genetic variation: undirected genetic erosion (genetic drift) caused by reduced spawning escapement and directed genetic change (selection) caused by fishing on particular components of the population. Both of them are easy to demonstrate theoretically and experimentally (e.g. Law 2000; Conover and Munch 2002; Tufto and Hindar 2003). However, there are few clear examples of loss of genetic variation in marine fisheries (Hauser *et al.* 2002; Hutchinson *et al.* 2003; Kenchington 2003; Olsen *et al.* 2004) and even fewer that we know of in salmon fisheries (Hard 2004; Consuegra *et al.* 2005a).

10.3.1 Undirected genetic erosion

The genetic diversity of most marine and anadromous fishes has generally been thought to be unaffected by exploitation because, even at 'collapsed' total population sizes, they are so numerous that changes in diversity are unlikely to occur (Crow and Kimura 1970). However, when a population is reduced from a very large to moderate size, which would have negligible

effect on heterozygosity or inbreeding (Chapter 8), genetic variation can still be lost, as the population will harbour a lower expected number of alleles per locus (Ryman *et al.* 1995). This may be significant, for example in some major loci such as the immune response genes (termed MHC, major histocompatibility complex) where adaptability seems to depend on a high number of alleles at a small number of loci (Chapter 7).

Loss of genetic variation through reduction in population sizes must be considered both at the level of individual populations (Wang *et al.* 2002a,b) and for several populations viewed together. For anadromous fishes being harvested together in the sea, the management problem is to optimise harvest while maintaining effective population size in several populations interconnected by migration. To study this, Tufto and Hindar (2003) developed a model using numerical methods to compute the total effective population size for a set of local populations with known population sizes and migration patterns. This was combined with a population dynamic model that includes the harvest rates of each population. The population dynamic/genetic model was used to investigate:

- how the biological reference points (e.g. spawning escapement) for a group of populations relates to river-specific reference points;
- how harvesting can be strategically used to minimise genetic loss; and
- how the population genetic structure affects the answers to these questions.

It is first necessary to understand the dynamics of effective population size in a group of interconnected populations (Box 10.1). Such a group of populations is what population geneticists refer to as a 'subdivided population' (Wright 1969), and what ecologists have termed a 'metapopulation' (Levins 1969). It is shown that low, symmetric migration rates between component populations increase the total effective size (relative to the component population sizes, Box 10.1). In some idealised situations, it is possible to relate the effective size of the total population to the sum of the effective component population sizes and the migration rate among the component populations. In the so-called finite island model of Wright (1969), where component populations of fixed effective size N_e exchange a fraction m through a common pool of migrants, the ratio of effective size to total component population size can be approximated by

$$N_e/(\Sigma N) \cong 1 + 1/(4Nm) \quad \text{(Waples 2002)} \tag{10.1}$$

From this it can be seen that the smaller the migration rate between subpopulations, the higher becomes the ratio between the total effective size and the sum of the local sizes.

Asymmetric migration, on the other hand, decreases the total effective size (Box 10.1). In the extreme case, that is, one-way migration, the total effective size eventually becomes equal to the effective size of the subpopulation emitting migrants (Tufto and Hindar 2003).

The second step to consider is the relationship between maximum sustainable yield (MSY) in a set of unconnected populations and MSY of the total population (Box 10.2). With deterministic population dynamics and full knowledge of each subpopulation, it is shown that the effect of migration can be ignored and the optimal harvesting strategy is to harvest each subpopulation to half of its carrying capacity (Tufto and Hindar 2003). This is the classical MSY solution applied to each subpopulation, and can be used as a starting point for setting 'conservation limits'.

By developing a model that maximises harvesting yield of a group of populations, subject to constraints set by maintaining the total effective size, Tufto and Hindar (2003) showed that:

- considerable gain can be made in total effective size in a group of populations when exploitation is based on knowledge about population structure;
- in source-sink population systems, the total effective size can be increased without reducing total harvesting yield by first reducing the harvest in the smallest population(s), while keeping the harvest in the largest population;
- when populations differ in their degree of isolation, it pays to harvest relatively less in isolated populations because these contribute more to the total effective size; and
- in cases with moderate or strong directionality in the migration pattern, the total effective size can become less than the sum of the subpopulation sizes.

10.3.2 Directed genetic change

Selective harvesting of fish populations potentially affects a number of ecological characters. Among these are body size, growth rate, age at maturity, reproductive effort, repeat spawning and run timing. These characters are known to vary both among and within Atlantic salmon populations (Nordqvist 1924; Taylor 1991), and part of this phenotypic variation has been shown to be heritable (Chapter 7). Moreover, when different components of a run consist of fish with different genotypic proportions, selection can act directly or indirectly on single-locus genotypes (Nelson and Soulé 1987).

The selective effects of fishing can be argued as follows (Law 2000): if a particular phenotype is selected in the fisheries and part of the phenotypic variation is heritable (e.g. body size, Gjerde 1993), then fishing causes evolutionary change. In quantitative genetic terms, the response to selection (R) is a function of the selection differential (S) and the heritability (h^2) of the trait:

$$R = h^2 \times S \tag{10.2}$$

where S is the difference between the mean phenotypic value after and before selection, and R is the difference between the mean value (before selection) in the current generation and the next generation (Falconer 1989).

Studies of selective harvesting have been motivated by the substantial changes in growth and maturation that have been observed in heavily exploited fish populations during the twentieth century (Law 2000). Such changes are important for yield and, thereby, fisheries management. If they cannot be satisfactorily explained by changes in the environment, selection due to exploitation may be a contributing factor. In that case, the possibility exists that fishing generates selection, causing evolution that changes the sustainable yield (Law 2000).

Experimental studies of both Atlantic salmon (Gjerde 1993) and Pacific salmon, e.g. chinook, *Oncorhynchus tshawytscha* (Hard 2004), show responses to selection for change in adult size and age at maturity. This clearly shows the potential for selective changes caused by a fishery that consistently targets a particular phenotype. It is, however, quite another task to demonstrate that the phenotypic changes observed in salmon populations reflect genetic changes caused by selection. Riddell (1986) discusses five reasons why realised responses to selection would be less than predicted from models of single-trait response. Among these are:

(1) limitations to data quality and/or the duration of monitoring change; (2) no additive variance for age at maturity in the wild; (3) the inability of single-trait models to account for genetic covariances among traits, or the inadequacy of the harvested portion of a population as a measure of selection intensity; (4) demographic optimisation models (Schaffer 2004) are inadequate to account for the realised response to selection; and (5) the tetraploid ancestry of salmonids is not accounted for and the association between genotype and phenotype is poorly understood. Some of these discussion points find support in long-term studies of growth rate (Friedland *et al.* 2000) and/or sea age distribution (Summers 1995) that indicate a strong environmental component to phenotypic change in salmon. Others, however, seem to be counteracted by careful studies that estimate genetic parameters from individually tagged fish released into nature (Hard 2004), and by documented changes in studies of species with a simple and invariant life history (Ricker 1981).

10.4 Fishing and effective population size: the evidence

In some species, overexploitation has led to local or global extinction (Hutchings 2001) which represents irreplaceable losses of genetic variation. The next point to consider is whether exploitation leads to a reduction of genetic diversity. Obviously, any harvesting that reduces the number of spawners will lead to a reduction in the effective population size, unless there are compensating mechanisms, e.g. in the spawning behaviour. In isolated, numerically small populations, this relates to the same phenomenon as small founder populations used in hatchery propagation (Chapter 11). A recent genetic study of a marine fish species, the New Zealand snapper, *Pagrus auratus*, even suggests that genetic variation (heterozygosity) declines significantly as a result of exploitation of an abundant species (Hauser *et al.* 2002). One reason why this could occur seems to be related to the effective population size in this species being as much as five orders of magnitude smaller than the census population size from fishery data. We are not aware, however, that loss of heterozygosity has been linked to harvesting in anadromous Atlantic salmon populations.

In ten rivers located along the Sognefjorden, western Norway, Hindar *et al.* (2004) attempted to model the total effective population size as a function of the effective population size in the most numerous population, the River Lærdalselva. This river used to harbour more than 60% of the spawners in this system (Sættem 1995), but has recently been infected by the parasite, *Gyrodactylus salaris*, which is likely to reduce the number of spawners in the Lærdalselva by 85% or more. Using the model developed by Tufto and Hindar (2003) together with estimates of local population sizes based on river-bank counts (Sættem 1995), and estimates of migration patterns from limited tagging and allozyme studies, it can be shown that the total effective size in this system is linearly related to the effective size of the R. Lærdalselva (Hindar *et al.* 2004). Moreover, as long as the system is dominated by one river population (which probably acts as a source emitting more migrants than it receives from the small neighbouring populations), the total effective size is not greatly dependent on whether the fishery takes place in the fjord or in the rivers. The latter finding should be used with caution, as this metapopulation approach does not take into account that subpopulations may show inbreeding effects (Lynch 1991) or genetic adaptations to local environments, such as timing of return to a particular river (Hansen and Jonsson 1991) or tributary (Stewart *et al.* 2002). The need to protect the smaller populations in the Sognefjorden is also supported

by the finding that one fish from each of these 'sink' populations, contributes more to the total effective size than one fish from the R. Lærdalselva (Hindar *et al.* 2004). Similarly, Consuegra *et al.* (2005b) found no evidence for a historical reduction in genetic diversity in an Iberian salmon population despite a drastic reduction in abundance. This finding was attributed to source-sink metapopulation dynamics and high levels of asymmetric gene flow.

10.5 Phenotypic and evolutionary changes in exploited populations

Pink salmon, *Oncorhynchus gorbuscha*, provide a classical example of the effects of fishing (Ricker 1981). Because of their uniform life history (all returning to spawn after 2 years, and all dying after spawning), changes in body size reflect growth changes only and are not complicated by changes in the age composition of the catch. Ricker (1981) found that the size (weight) of pink salmon maturing in even-numbered years decreased from 2.1 to 1.4 kg between 1951 and 1975 (32 g/year) and that those maturing in odd-numbered years decreased from 2.5 to 2.0 kg (19 g/year). Pink salmon are caught by gill nets, seine nets and by trolling, and it appears that the decline in body size started when gill-netters shifted to a larger mesh size after new market policies from 1945 onwards made large-sized fish more valuable. Environmentally induced changes are unlikely, as a more intensive fishery should result in less dense populations and increased, rather than decreased, individual growth rate. The size difference between the pink salmon harvested and those available to the fishery (the selection differential) was compared with the observed decrease in size (the response to selection, if all of the decrease resulted from selection), giving a ratio of 0.22 for odd years and 0.30 for even years (Ricker 1981). These figures represent estimates of heritability (eqn 10.2) that lie within the range of heritabilities of body size in rearing experiments (Gjerde 1993; Hard 2004).

Similar evidence of size and/or age at maturity being affected by selective harvesting exists for other species (e.g. whitefish, cod, whiting) although perhaps less convincing than for pink salmon (Law 2000). In sockeye salmon, *Oncorhynchus nerka*, a massive numerical decline in anadromous sockeye in Lake Dal'neye between the 1930s and 1970s coincided with an increase in the proportion of fish maturing in fresh water without going to sea (see Thorpe 1993). Moreover, Altukhov and Salmenkova (1991) noted a higher enzyme heterozygosity in early maturing males, suggesting that oceanic fishing affected life history as well as molecular genetic characteristics of the population. In chinook salmon, a species with a life history not very different from Atlantic salmon, Hard (2004) showed through a quantitative genetic study of a large-scale crossing and release experiment that strong directional selection on body size was likely to produce modest short-term reductions in size. The magnitude of this effect depended (among other factors) on harvest rate, harvest size threshold (i.e. minimum size captured by the nets), and the strength of stabilising natural selection on size. Another important result was that disruptive selection, which would occur if the fisheries captured an intermediate window of the size distribution, could substantially reduce the strength of selection on size (Hard 2004).

Considerable evidence exists from Atlantic salmon populations that fishing captures a non-random portion of the population. For example, some Spanish populations, that have been harvested by rod-and-line only for the last 50 years, show significant differences between the size of fish caught and the spawning population (Consuegra *et al.* 2005a; Table 10.2). Also, these rivers show a long-term decline in the body size of salmon (Fig. 10.5). Moreover,

Table 10.2 Phenotypic and genetic traits of Atlantic salmon that are actually or potentially affected by selective harvesting.

Trait	Observed change attributed to selective harvesting	Reference
1. Timing of entry into the river	Delayed entry	Consuegra *et al.* (2005*a*)
2. Adult body size	Reduction in average size	Schaffer & Elson (1975) Gee & Milner (1980) Bielak & Power (1986) Consuegra *et al.* (2005a)
3. Age structure	Increased smolt age	Ritter & Newbould (1977) Consuegra *et al.* (2005a)
	Increased incidence of grilse	Schaffer & Elson (1975) Gee & Milner (1980) Consuegra *et al.* (2005a)
4. Life-span	Reduced life span and longevity	Consuegra *et al.* (2005a)
5. Sexual maturation	Increased incidence of mature male parr Maturation at earlier ages	Caswell *et al.* (1984) Porter *et al.* (1986) Wohlfarth (1986) Consuegra *et al.* (2005a)
6. Allozyme variation	Change in MEP-2* frequencies	Consuegra *et al.* (2005a)
7. mtDNA variation	Change in ND1/16sRNA haplotypes	Consuegra *et al.* (2005a)
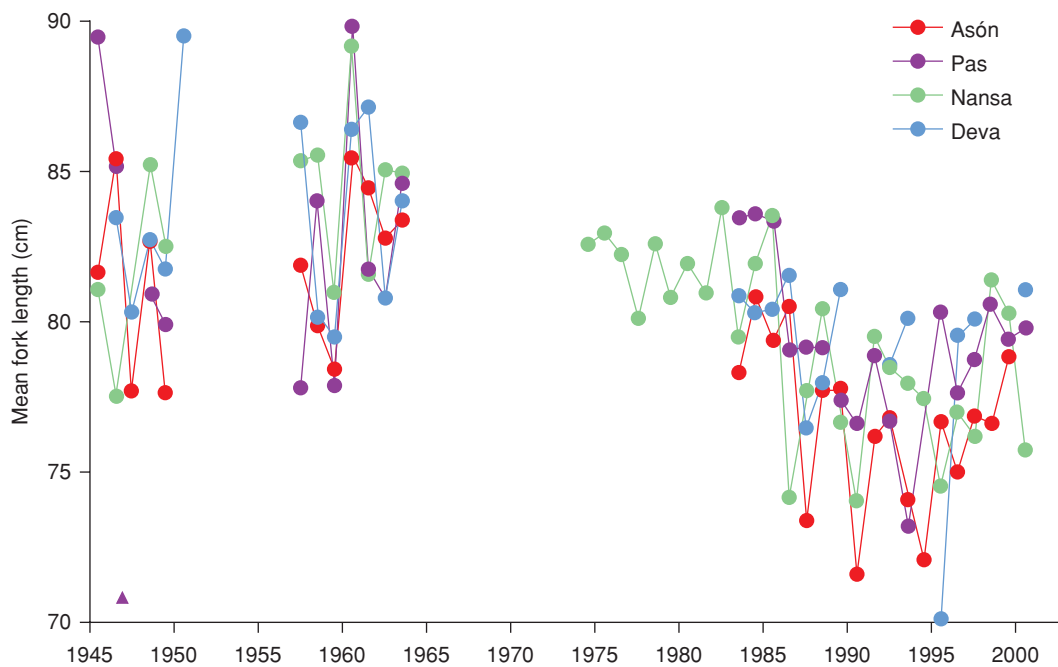
Fig. 10.5 Historical trends in the average size of Atlantic salmon caught by anglers in four Iberian populations exploited during a fairly constant fishing season from February/March to July. Based on García de Leániz *et al.* (2001).

Table 10.3 Reared smolts released as 2+ in Imsa 1981 and recaptured as 1SW fish in coastal fishery and in river trap (data based on Hansen 1984).

Stock	Sea fishery		Caught in trap		Proportion caught in fishery	Est. wt. before fishery	Selection differential	Predicted response
	weight	N	weight	N				
Lone	1.76	40	1.55	68	0.37	1.63	−0.08	−0.03
Imsa	2.54	213	2.35	114	0.65	2.47	−0.12	−0.04
Figgjo	2.60	201	2.26	79	0.72	2.50	−0.24	−0.09
Suldal*	2.94	46	2.49	15	0.75	2.83	−0.34	−0.12
Sandvika*	2.96	118	2.69	33	0.78	2.90	−0.21	−0.08
Alta*	3.15	155	2.72	11	0.93	3.12	−0.40	−0.14
Eira*	3.28	49	2.68	7	0.88	3.21	−0.52	−0.19
Årøy*	3.42	33	3.19	7	0.83	3.38	−0.19	−0.07

* Multi-sea-winter stock.

calculation of the selection differential on body size of released salmon returning as 1SW fish to the Imsa in Norway (Hansen 1984; Table 10.3) suggests that strong directional selection could act on this trait (ignoring that some of these populations mature largely as MSW salmon). For example, three 1SW populations were predicted to decline by 30–90 g per generation by the coastal fishery alone (Table 10.3).

Changes in numbers and phenotype of Norwegian salmon populations were recorded following the cessation of the Norwegian drift net fishery in 1989 (Jensen *et al.* 1999). Drift nets are known to select large-sized 1SW fish and small-sized MSW salmon. In three out of four rivers, the catches of 1SW salmon increased and their mean weight increased in all four rivers. Higher sea ages were less affected. In Russian rivers draining to the Barents Sea, a similar but less obvious trend was found, whereas White Sea populations showed no change. These results showed good correspondence to actual drift-net selectivity curves and the mean weights of drift-net catches.

Nevertheless, it should be noted that one of the best-documented declines in adult body size of Atlantic salmon (Friedland *et al.* 2000) is more likely to be a result of changing environmental conditions in the sea. Another impressive data set, showing parallel, long-term trends in the proportion of 1SW fish in several eastern Scottish rivers (Summers 1995), is also likely to show an environmentally induced effect, the causative agent being unknown. It remains a challenge, therefore, to demonstrate phenotypic changes in Atlantic salmon populations that are best interpreted as a response to selection. An inability to demonstrate a response to selection does not imply that fisheries selection is unimportant, and is likely to be caused mainly by inadequate data (see Riddell 1986) because major changes in the fishery have taken place within a few salmon generations.

On the River Spey in Scotland, tagging of rod-caught fish and monitoring of subsequent recaptures indicates re-exploitation rates of ~ 30% for fish caught first, for example, in February and March, but re-exploitation rates of only < 2% for fish caught in July and August. Differences in re-exploitation rate appear to depend partly on seasonal differences in intrinsic catchability and partly on the duration of the period over which post-entrant fish remain catchable (J. Thorley, pers.comm.). Radio-tracking studies on a number of rivers (Webb and Campbell 2000) demonstrate that run timing and spawning location are spatially correlated, with earlier-running fish spawning at higher elevations that are generally more

distant from the sea. Since sub-catchment populations spawning in the upper parts of catchments tend to comprise early-running fish, they are therefore susceptible to higher exploitation rates than those spawning in down-river locations.

In addition, early-running fish have suffered particularly marked recent declines in abundance, probably due to differential rates of marine mortality (Youngson *et al.* 2003). Reduced abundance, coupled with high intrinsic catchability, means that, under current conditions, spawning populations of early-running fish are particularly susceptible to overexploitation by rod fisheries. It follows that corresponding latitude exists, under conditions such as those that apply at present, for anthropogenic effects on the relative strength of different spawning populations, even when they are exposed to constant rates of rod fishing effort throughout the fishing season. These considerations have a well-defined genetic aspect since run timing (and therefore exploitation rate, escapement rate and local spawning adequacy) is strongly affected by the genetic characteristics of the populations (Hansen and Jonsson 1991; Stewart *et al.* 2002).

10.6 Future management of salmon fisheries

Genetic considerations in fisheries resemble in many ways the considerations that would arise from hunting. Harris *et al.* (2002) reviewed the potential effects of hunting on terrestrial vertebrates, and saw no urgency as they found only a few documented cases of undesirable genetic consequences. Against this background, harvesting of salmon seems to represent a smaller threat to the genetic constitution of Atlantic salmon populations today than gene flow from escaped farm salmon invading wild populations to spawn (Chapter 12), and habitat degradation (WWF 2001).

Nonetheless, the recent collapse of some of the world's major fish stocks and the 30-year-long decline of wild Atlantic salmon populations suggests that a precautionary approach be taken to salmon management (NASCO 1998; Crozier *et al.* 2003). To this end, a better ability to judge whether spawning escapement is above a threshold necessary to secure long-term population viability, is a first step. A good example is the recent catch advice provided for Irish fishing districts, based on estimates of pre-fishery abundance and stock-recruitment relationships for Irish rivers (Ó Maoiléidigh *et al.* 2004). Secondly, the potential for selective changes should be considered by salmon managers (Table 10.4). Selection should be considered when

Table 10.4 Some possible consequences of fishery regulations and how they can lead to selective harvesting of Atlantic salmon populations.

Regulation	Possible consequences
1. Catch quotas	Fish in excess of catch quotas are not exploited by the fishery
2. Regulation of fishing gear (lines, lures, nets)	Individuals can vary in their vulnerability to the fishery, depending on body size, sex, activity, etc.
3. Size limits	Small fish can be underexploited while large, trophy fish can be overexploited (or vice versa)
4. Fishing areas and fishing effort	Some fish are overexploited while others are underexploited due to unequal spatial distribution of fishing effort
5. Fishing season and fishing times	Early fish are overexploited while late fish are underexploited due to unequal temporal distribution of fishing effort

designing new regulations for river and coastal fisheries: for example, size limits and fishing season in relation to run timing of different population components (Stewart *et al.* 2002; Consuegra *et al.* 2005a). Selective changes towards sexual maturation at a smaller body size should be a prime concern, as they have implications for population fecundity (see Olsen *et al.* 2004). Finally, strong spawning populations of wild Atlantic salmon should always be considered as a buffer against natural and human-made environmental factors that threaten the viability and genetic integrity of Atlantic salmon populations.

10.7 Summary and conclusions

- Fishing can result in loss of genetic diversity by selectively removing species and populations, and by causing undirected and directed changes within populations.
- Microevolution caused by fishing may be important even when masked by other factors.
- Run timing and body size are prime candidates for studies of genetic response to selective fishing.
- Genetic responses in life-history characters (e.g. age at maturity) are notoriously difficult to demonstrate.
- Isolation increases total effective population size whereas asymmetry in gene flow (and population size) decreases it.
- If population sizes and patterns of gene flow (or genetic structure) are known, harvesting can be used strategically to increase total effective size without much loss of yield.
- Harvesting of salmon populations today seems to represent a smaller threat to the genetic constitution of these populations than gene flow from escaped farm salmon, and habitat degradation.

10.8 Management recommendations

- The management of salmon fisheries needs to take into account the genetic effects caused by reduced population size, as well as those caused by selectively removing populations or population components.
- Undirected (random) loss of genetic diversity should be considered at the single-population level as well as at the level of a set of interconnected populations.
- Knowledge about local population sizes and migration patterns, or alternatively, studies of the genetic structure of the species, should be used to assess the relationship between local effective population sizes and the effective size of the total population.
- Care should be taken to avoid selective fishing on population components that have a hereditary basis.
- Reduced harvesting can be used strategically to avoid (or reduce) genetic effects of other factors affecting salmon populations.

Box 10.1 Effective population size in a subdivided population (Tufto and Hindar 2003).

Consider a two-population system, each having a local effective population size of 10, and symmetric migration so that subpopulation 1 receives 1% migration from subpopulation 2 and vice versa. For this population system, the total effective population size becomes $N_e = 38.7$, that is, almost twice as high as the sum of the local effective sizes. For the same population system but with free interbreeding between the two subpopulations (panmixia, which corresponds to migration rates equal to 50%), the total effective population size becomes $N_e = 20.5$, approximately equal to the sum of the local effective sizes.

In situations with asymmetric migration, the total effective population size can become greatly reduced. Consider the same two-population system with local effective sizes of 10, but where subpopulation 1 receives 10% migration from subpopulation 2 and subpopulation 2 receives 1% from subpopulation 1. For this system, we get $N_e = 13.2$. Here, the total effective population size is not much higher than the size of one of the subpopulations. In the extreme case of one-way migration, the fate of the two-population system will be completely governed by the subpopulation emitting migrants and the total effective size equal to the effective size of this donor population.

The effective population size of any pattern of migration can be computed. As long as subpopulations are of constant size over time, the only limitation of this approach is the amount of computer memory needed (proportional to n^4) and central processing unit time (proportional to n^6). For example, for a system of $n = 40$ subpopulations, the numerical computations involve 820×820 matrices (for details, see Tufto et al. 1996).

Box 10.2 Maximum sustainable yield in a subdivided population (Tufto and Hindar 2003).

We consider a simple population dynamic model where the change in population size in subpopulation i is given by

$$\Delta N_i = r_i N_i \left(1 - \frac{N_i}{K_i} \right) - Y_i(N_i) - N_i + \sum_{j=1}^{n} \tilde{m}_{ij} N_j \tag{10.2.1}$$

The first term on the right-hand side is the standard Lotka–Volterra logistic growth model, where r_i is the intrinsic growth rate and K_i is the carrying capacity of subpopulation i. The second term represents the annual reduction in population size as a result of the chosen harvesting strategy. The two last terms represent emigration and immigration. Note that $\tilde{m}_{ij}$ is the probability that an individual migrates to subpopulation j given that it originates from subpopulation i, which gives the entries of the forward migration matrix (as opposed to the backward migration matrix above). It follows (see Tufto and Hindar 2003 for details) that the total yield from the population can be written

$$Y(N_1, N_2, \ldots, N_n) = \sum_{i=1}^{n} r_i N_i \left(1 - \frac{N_i}{K_i} \right) \tag{10.2.2}$$

that is, the effect of migration can be ignored and the optimal harvesting strategy with no constraints on the effective size is to harvest each sub-population to half of its carrying capacity such that $N_i = K_i/2$.

Our primary interest here is in the optimal solution for harvesting with constraints on the total effective size. We want to maximise (10.2.2) subject to the constraint

$$N_e(N_1, N_2, \ldots, N_n) - N_e^* = 0 \tag{10.2.3}$$

where N_e^* is the chosen required total effective size. This problem must be solved numerically. Details are given in Tufto and Hindar (2003).

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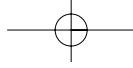
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