A metapopulation perspective for salmon and other anadromous fish

Nicolas Schtickzelle[1,2] *& Thomas P. Quinn*[2]

[1]Biodiversity Research Centre, Université Catholique de Louvain, 4 Place Croix du Sud, B-1348 Louvain-la-Neuve, Belgium; [2]School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA

Abstract

Salmonids are an important component of biodiversity, culture and economy in several regions, particularly the North Pacific Rim. Given this importance, they have been intensively studied for about a century, and the pioneering scientists recognized the critical link between population structure and conservation. Spatial structure is indeed of prime importance for salmon conservation and management. At first glance, the essence of the metapopulation concept, i.e. a population of populations, widely used on other organisms like butterflies, seems to be particularly relevant to salmon, and more generally to anadromous fish. Nevertheless, the concept is rarely used, and barely tested.

Here, we present a metapopulation perspective for anadromous fish, assessing in terms of processes rather than of patterns the set of necessary conditions for metapopulation dynamics to exist. Salmon, and particularly sockeye salmon in Alaska, are used as an illustrative case study. A review of life history traits indicates that the three basic conditions are likely to be fulfilled by anadromous salmon: (i) the spawning habitat is discrete and populations are spatially separated by unsuitable habitat; (ii) some asynchrony is present in the dynamics of more or less distant populations and (iii) dispersal links populations because some salmon stray from their natal population. The implications of some peculiarities of salmon life history traits, unusual in classical metapopulations, are also discussed.

Deeper understanding of the population structure of anadromous fish will be advanced by future studies on specific topics: (i) criteria must be defined for the delineation of suitable habitats that are based on features of the biotope and not on the presence of fish; (ii) the collection of long-term data and the development of improved methods to determine age structure are essential for correctly estimating levels of asynchrony between populations and (iii) several key aspects of dispersal are still poorly understood and need to be examined in detail: the spatial and temporal scales of dispersal movements, the origin and destination populations instead of simple straying rates, and the relative reproductive success of immigrants and residents.

Keywords conservation and management, metapopulation dynamics, population structure, salmon, spatial structure, trout

Introduction

Anadromous salmonids are an important component of biodiversity, culture and economy in several regions, particularly the North Pacific Rim (National Research Council 1996; Quinn 2005 and references therein). They link freshwater and saltwater ecosystems by carrying nutrients from the sea, where they grow, to the lakes and tributaries, where they die after spawning. Flooding and the action of bears and other animals move these nutrients to the nearby terrestrial ecosystems, further expanding the ecological influence of salmon (Gende *et al.* 2002). Salmon and related species such as trout, here referred to collectively as salmon for simplicity, are therefore keystone species for these generally nutrient-poor temperate and northern ecosystems (Willson and Halupka 1995; Naiman *et al.* 2002). Furthermore, salmon have always played an important role in human culture, both for native peoples and more recent settlers. Last but not least, salmon are extremely important economically, generating billions of dollars through commercial and recreational fisheries. Given this importance, salmon have been intensively studied for about a century, and the pioneering scientists recognized the critical link between population structure and conservation (Rich 1939).

As habitat loss, degradation and fragmentation are among the most serious threats to biodiversity (Wilcove *et al.* 1998; Pimm and Raven 2000), the metapopulation concept has been embraced in conservation biology and management (Hanski and Simberloff 1997). A metapopulation is broadly defined as a collection of local populations inhabiting discrete patches of suitable habitat, interacting through dispersal and persisting in a balance between stochastic extinctions and recolonizations (Hanski and Gilpin 1997; Hanski 1999 and references therein). This concept greatly advanced our understanding of the consequences of habitat fragmentation, as distinct from habitat loss (Hanski 1989; Hanski and Gilpin 1991), and it helped design conservation guidelines for species whose habitat is naturally or artificially fragmented (Hanski 2002).

At first glance, the essence of the metapopulation concept seems to be particularly relevant to anadromous fish in general, and especially salmon as detailed in this paper. Nevertheless, only 0.25% of the papers on conservation and/or management of salmonids list the keyword 'metapopulation', i.e. the lowest proportion among several types of organisms (Table 1). We see two possible explanations for this paradox. On the one hand, the strong tendency of salmon to home (Quinn 1993) may have been responsible for a vision of salmonid spatial structure as a collection of nearly isolated populations (Hill *et al.* 2002). In this conception, straying is perceived as an exceptional event, because of some failure of imprinting and homing (Cury 1994); the prevalent use of the word 'straying' with a maladaptive connotation, instead of 'dispersal', denotes this fact. On the other hand and quite conversely, many people involved in the conservation and management of salmonids are well aware of the importance of interactions between populations, but refrain from using the concept and the term 'metapopulation'. Such reticence has been supported by some researchers (Smedbol *et al.* 2002; Kritzer and Sale

Table 1 Summary of published literature, revealing the paucity of papers about salmonid conservation referring to the metapopulation concept.

Keyword(s)	Conservation or management, and metapopulation[a]	Conservation or management	Proportion citing metapopulation (%)
Salmonids: (trout[a] or salmon[a])	89	36 207	0.25
Fish: (fish[a])	310	101 911	0.30
Mammals: (mammal[a])	377	100 461	0.38
Birds: (bird[a])	344	87 131	0.39
plants: (plant[a])	515	107 715	0.48
Butterflies: (butterfl[a])	378	4 625	8.17

[a]A wildcard replacing 1 or more letters.
Source: ISI Web of Knowledge CrossSearch (available on http://www.isiknowledge.com; databases: Web of Science, BIOSIS Previews, Zoological Record; Timespan = 1965–2007; accessed on 09/01/2007).

2004) given the paucity of data on metapopulation structure in the marine environment, but may also be due to historical reasons, or a combination of the two. The metapopulation theory was indeed developed on other kinds of organisms, especially butterflies, while other concepts have become established for salmon, notably the evolutionarily significant unit (ESU: Waples 1991; Fraser and Bernatchez 2001). In addition, the importance of salmon population structure has been understood for decades (Ricker's 1972 review), and terminology and perspectives were thus set long before the metapopulation concept was developed. Both metapopulation and ESU are concepts of spatially structured populations, but they differ in the intensity and time scale of dispersal. In a metapopulation, dispersal typically occurs at relatively short-time scales (ecological time) affecting population dynamics. For an ESU, the importance of dispersal typically arises, however, at longer-time scales (evolutionary time) allowing gene flow across the entire unit.

Many authors using the term 'metapopulation' in their work on salmon pre-suppose that metapopulation dynamics have always been obvious and demonstrated: 'salmonid metapopulations are sometimes taken for granted' (Rieman and Dunham 2000 p. 54). It seems that the occurrence of dispersal is equated with the existence of metapopulation processes and dynamics, without any further assessment. Often, authors do not refer to any data or previous study when stating that metapopulation structure exists in their system (Candy and Beacham 2000; Jager *et al.* 2001). This suggests that many people working on fish may not fully understand the metapopulation concept, even if the term is familiar to them (Smedbol *et al.* 2002). Altogether, there have been very few attempts at assessing the potential existence and/or importance of metapopulation dynamics for salmon based on field data; but see the work by Rieman and Dunham (2000) on non-anadromous species or the use of microsatellites on Atlantic salmon (*Salmo salar*, Salmonidae) (Garant *et al.* 2000).

The question of metapopulation dynamics in anadromous fish is not simply a rhetorical or semantic exercise. Issues concerning spatial and metapopulation dynamics are of direct interest to the managers (Fromentin and Powers 2005), who must prioritize watershed conservation and restoration efforts, and regulate fisheries. There are two main reasons for this importance. First, metapopulation dynamics might influence the persistence of fish populations, both at the ecological time scale, affecting which populations are likely to collapse (Hill *et al.* 2002), and at the evolutionary time scale, through the capacity for evolution and adaptation (Hilborn *et al.* 2003). Indeed, fragmentation and its numerous deleterious effects (Fahrig 2003 and references therein) may be more serious for stream-living organisms than for many terrestrial organisms because dispersal can only occur along the one dimensional path of the stream, as opposed to the two or three dimensions for terrestrial species. Second, dispersal and metapopulation dynamics might weaken the link between local abundance, a primary input used in fisheries management (Hilborn and Walters 1992), and local demography. A habitat with poor local reproduction but a high abundance because of immigration from nearby populations would be interpreted as a high quality habitat if the importance of dispersal was over-

looked (Gowan and Fausch 1996; Cooper and Mangel 1999; McElhany *et al.* 2000). Similarly, attempts to relate abundance/occurrence to habitat characteristics without accounting for the effects of metapopulation dynamics might be misleading (Dunham and Rieman 1999).

Patch occupancy surveys, using snapshots of the presence/absence of a species in a collection of habitat patches, have been used to assess the existence of metapopulation dynamics for a variety of animal species (Hanski 1998). Metapopulation dynamics are inferred when the presence of the species is correlated to patch size and connectivity; large patches are more likely to be occupied than small patches, well connected patches more than isolated patches (Dunham and Rieman 1999; Koizumi and Maekawa 2004). Metapopulation dynamics are also inferred when colonization and extinction probabilities are correlated with the fraction of occupied patches (Gotelli and Taylor 1999). However, these approaches present two main disadvantages. First, many types of metapopulations can exist without substantial and rapid population turnover (extinctions/recolonizations) (Kritzer and Sale 2004) or without a fraction of the suitable habitats being vacant (see below) (Baguette 2004). Second, in many cases of patch occupancy surveys, there is no direct evidence that between-patch dispersal is the process responsible for the occupancy pattern, and processes other than metapopulation dynamics can generate similar patterns (Clinchy *et al.* 2002).

The aim of this paper is to present a metapopulation perspective for anadromous fish, by assessing the set of necessary conditions for metapopulation dynamics in terms of processes rather than of patterns. We first summarize the metapopulation concept and the conditions under which systems are likely to exhibit metapopulation dynamics. We then review the applicability of the concept to the representative case of the salmonids. Finally, we discuss some areas where further research is needed. We have largely focused our attention on the sockeye salmon (*Oncorhynchus nerka*, Salmonidae) in Bristol Bay, Alaska, with the intent to provide a clear illustration of all the ideas developed on a single case. However, the framework we present clearly extends to other anadromous fish and other regions, e.g. Atlantic salmon, but to keep this perspective manuscript concise, we have limited references for these other cases to only a few of the key papers.

The metapopulation concept

The term 'metapopulation' was coined more than three decades ago by Levins, who defined it as a population of populations which go extinct locally and recolonize (Levins 1969, 1970), paralleling a population with births and deaths of individuals. After 20 years of dormancy of the concept, the founder book 'Metapopulation dynamics: empirical and theoretical investigations' (Gilpin and Hanski 1991) marked the real start of metapopulation biology. Since then, metapopulation theory has been formalized and developed in many directions (Hanski and Gilpin 1997; Hanski 1999; Hanski and Gaggiotti 2004 and references therein).

From the relatively narrow Levins concept, i.e. independent and identical populations, our present view of metapopulations has broadened (Harrison 1991, 1994; Hanski and Gilpin 1997; Harrison and Taylor 1997): 'any assemblage of discrete local populations with migration among them is considered to be a metapopulation, regardless of the rate of population turnover' (Hanski and Gilpin 1997 p. 2). The current metapopulation theory gives to space, i.e. the spatial structure of populations, a role of prime importance in the dynamics of animal and plant populations. Metapopulation theory has introduced the idea that the long-term persistence of a metapopulation cannot be explained only by the persistence of the local populations it consists of, but depends also on regional processes of (re)colonization and extinction. In other words, metapopulation dynamics depend on immigration and emigration, as population dynamics do on births and deaths. Individuals (local populations) die but are replaced by new ones, and the population (metapopulation) persists far longer than any of its individuals (local populations). The dynamics of a metapopulation are the result of local dynamics and regional (metapopulation *sensu stricto*) dynamics; local dynamics depend on habitat patch size and quality, regional dynamics depend on landscape configuration, i.e. habitat patch position, connectivity, and large-scale environmental forcing. The balance between these two levels of dynamics, local and regional, depends on various features of the patch network and of the species.

To satisfy the metapopulation concept, a network of habitat patches must meet three basic conditions (Hanski *et al.* 1995; Hanski and Gilpin 1997, Fig. 1): (i) the local populations inhabit discrete habitat patches, well separated from the rest of the
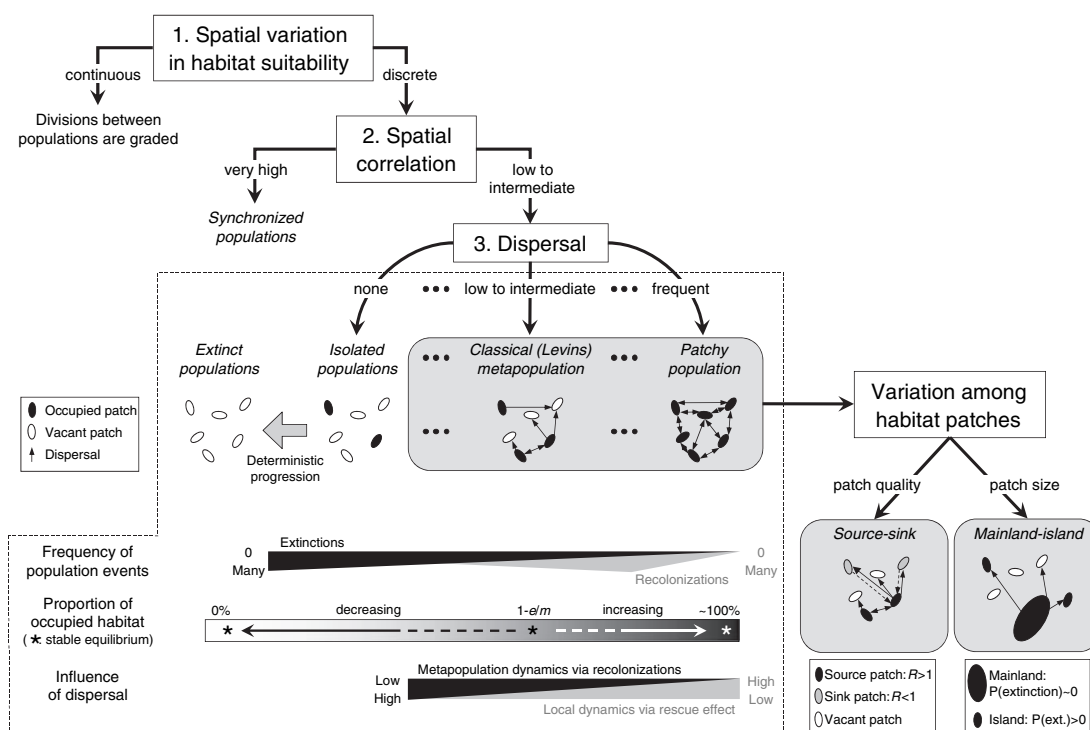
Figure 1 Schematic representation of the three main conditions necessary for metapopulation dynamics to occur; the variation in habitat patch size and/or quality is not a condition but is responsible for specific properties of metapopulation systems. Metapopulation theory is useful for cases with grey shading. The main types of (meta)populations defined in the current classification are indicated in italics (see references in the text). The dashed line insert describes the variation of three properties of (meta)population systems along the continuum of dispersal magnitude. e, local population extinction rate; m, local population recolonization rate; R, population growth rate in the absence of dispersal.

landscape, the latter being unsuitable for the species and called the matrix. When the variation in habitat quality is graded rather than discrete, the delineation of habitat patches and populations is unclear, and the metapopulation theory is inapplicable, (ii) there is some asynchrony between dynamics of local populations, making simultaneous stochastic extinction of all local populations very unlikely. With perfectly synchronized populations, metapopulation persistence is not higher than the persistence of any one of the local populations and (iii) the habitat patches are not too isolated to prevent dispersal events. Without dispersal, the dynamics of populations are purely local, no metapopulation processes can occur, and the long-term persistence is lower.

When these three conditions are met, the system may function as a metapopulation, and current metapopulation theory is likely to be of interest in the study of its dynamics and viability. Two major elements determine the type of metapopulation for a given system: the magnitude of dispersal, and the

spatial variance in the size and quality of habitat patches. Figure 1 illustrates these basic situations and makes the link with the established classification of metapopulation systems (Hanski and Gilpin 1991; Harrison 1991; Thomas and Hanski 1997). Real metapopulations are most likely to straddle several types and to combine specific features of each type; the spatial scale at which one looks also influences the type of structure that fits best (Harrison and Taylor 1997). Nevertheless, the information presented in Fig. 2 helps to classify a particular network of populations and thereby determine the processes likely to be important in its dynamics and persistence.

The magnitude of dispersal for a given species in a given landscape depends on the ability of emigrants to move through the particular landscape elements and habitat types and reach another suitable habitat patch. This is the result of the interplay between physical features of the landscape and species attributes concerning movement behaviour

and mobility, and is directly related to travel costs, either direct, i.e. mortality, or deferred, e.g. loss of time for reproduction in the destination patch (Stamps *et al.* 2005; Van Dyck and Baguette 2005). In other words, even in the same landscape different species may present different levels of functional connectivity, i.e. 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor *et al.* 1993). Conversely, populations of the same species may vary in dispersal, depending on features of the landscape (Wiens 2001; Schtickzelle *et al.* 2006). The importance of dispersal in a spatially structured network of populations depends on the magnitude of dispersal, both in temporal frequency and spatial extent, relative to the frequency of local extinctions and the speed of local dynamics (Fig. 1). The equation of the Levins model (Levins 1969, 1970) is a simple illustration of the systems arising along this continuum of dispersal from isolated populations to a patchy panmictic population. The rate of change through time of the fraction p of patches occupied at any time t is given by:

$$\frac{dp}{dt} = mp(1 - p) - ep \qquad (1)$$

Where m and e are the colonization and extinction probabilities respectively. When the frequency of recolonizations through dispersal is consistently high enough to balance the frequency of local extinctions at the landscape scale ($e/m < 1$), the system is in a stable equilibrium ($dp/dt = 0$), with only a fraction $p* = 1 - e/m$ of the habitat occupied; this is the case in the classical metapopulation models. At one end of the continuum of dispersal magnitude, when recolonizations are not frequent enough to balance local extinctions ($e/m \geq 1$), the system is in a non-equilibrium state and is declining towards extinction. This may happen, for example, when habitat destruction increases the frequency of extinctions or decreases the connectivity, limiting recolonizations, because there is a delay before the system reaches its new equilibrium at extinction, the so-called 'extinction debt' (Tilman *et al.* 1994). At the other end of the continuum, dispersal may occur more frequently than local events causing population fluctuations. In this case, populations may receive enough immigrants to prevent local extinctions ($e/m \sim 0$; the so-called 'rescue effect': Brown and Kodric-Brown 1977). As a consequence, the species tend to occupy all the suitable habitats ($p* \sim 1$). In this case, dispersal may strongly influ-

ence local population dynamics (Stacey *et al.* 1997) and synchronize the temporal variations of population dynamics (Liebhold *et al.* 2004), resulting in a patchy population. The incidence of dispersal may vary between spatial scales. If some parts of the system are less connected than the average in the system, e.g. those patches in the marginal part of the network, then they may receive fewer immigrants and their emigrants may encounter a higher mortality during dispersal. This creates a hierarchy of subnetworks with different structures, e.g. a core area of well-connected patches functioning as a patchy population surrounded by less connected patches functioning like a metapopulation (see Schtickzelle and Baguette 2004 for an example on a butterfly species).

New considerations are needed if habitat patches differ significantly in local features. When some local populations are far bigger than the others, for example because they occupy very large habitat patches, they are likely to have a very low probability of extinction; indeed, all other things being equal, extinction probability is a function of population size (Lande 1993). The persistence of such systems, called mainland-island or core-satellite and derived from the MacArthur and Wilson model of insular biogeography, is largely determined by the persistence of the large population(s) (Boorman and Levitt 1973); most local extinctions will be unimportant for the metapopulation persistence because only small populations are affected. When the quality but not the size of the habitat patches is different, population growth in the absence of dispersal may be different: sources exhibit intrinsic positive growth (reproduction > mortality), sinks negative (reproduction < mortality) (Pulliam 1988; Dias 1996). Sinks are therefore doomed to extinction if not rescued by immigrants from a source population, whereas sources can persist without immigration from other populations. There are no assumptions regarding the relative abundance of individuals in source and sink populations; sinks could have larger populations than sources.

Application to anadromous salmonids

How do these concepts apply to salmon? In this section, we review the literature for general information about life history traits, with a special focus on the example of sockeye salmon in Bristol Bay, south-western Alaska (Fig. 2a). In this region, a collection of lake systems and associated streams and
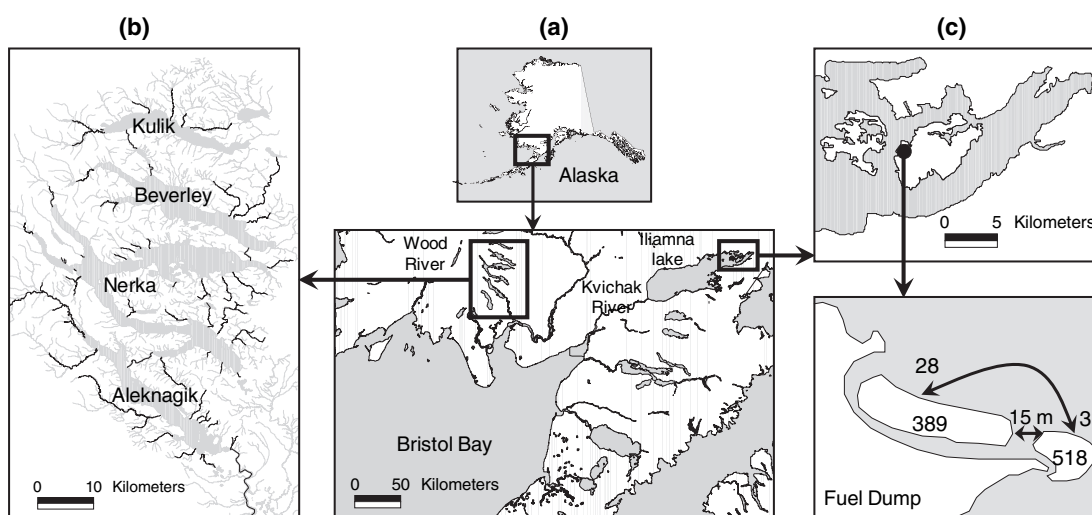
Figure 2 Condition 1: habitat is discrete. (a) Map of Bristol Bay, Western Alaska, USA. (b) The Wood River system. The five major lakes and associated streams are shown in grey and major sockeye salmon spawning grounds are shown in black. (c) Fuel Dump Island sockeye salmon spawning ground, with number of observations of males staying in the bay, staying in the point, and moving between the bay and the point (data from Hendry *et al.* 1995). Source of GIS data: Alaska Department of Natural Resources, Land Records Info. Section, 1984, Alaska Coastline 1:250 000, General Base Map Alaska, ADNR, LRIS, Anchorage, AK.

rivers provide the spawning habitat for sockeye and other Pacific salmon species. These lake systems are largely in their pristine state, with only minimal habitat degradation, unaffected by agriculture, logging or dam building for hydroelectric power production. There are no hatcheries, and fisheries, the only important human impact on salmon in Bristol Bay, have proven to be sustainable (Hilborn *et al.* 2003). The fisheries are carefully managed by the Alaska Department of Fish and Game to ensure that enough mature salmon escape harvest to keep the systems at or near their carrying capacities; this management involves a target for the number of returning adults that are needed to reach the carrying capacity of each system, determined from a mix of stock-recruitment relationships and habitat features (Minard and Meacham 1987). The variation in abundance caused by fishing is less than that caused by natural processes (Hilborn *et al.* 2003). Anthropogenic perturbations of local and metapopulation dynamics, if any, are thus likely to be quite limited.

Is the habitat discrete?

The first question relevant to metapopulation dynamics is to determine whether the habitat is discrete or continuous (Fig. 1). While some flexibility exists, metapopulation theory is not applicable in

cases where habitat suitability varies continuously because the divisions between local populations are graded rather than discrete in such a situation.

The habitat is normally the place where the species completes its life cycle, i.e. the set of biotopes used by some or all life stages to find resources they need. For many species, one biotope offers all the resources needed to complete the whole life cycle, and the definition of habitat is quite straightforward. For anadromous fish, different stages occupy totally distinct biotopes, sometimes thousands of kilometres apart. In the case of sockeye salmon, lake beaches, outlet rivers and tributaries are used for reproduction and development of embryos, large rivers are used as down- and upstream migration corridors, and the open ocean is the region where most growth takes place. Sockeye salmon differ from other Pacific salmon in that lakes are used for rearing by juveniles rather than streams. Each of these biotopes is vital for the species but reproduction is the key for the definition of the population concept: a set of potentially interbreeding individuals (Schaefer 2006). Therefore, the habitat associated directly to the delineation of anadromous fish populations is the spawning ground.

Spawning habitat is clearly discrete in the case of salmon (Quinn 2005 and references therein). Only some rivers, streams and lake beaches are suitable for spawning, and these are separated by stretches

of land or deep water, unsuitable for spawning (Fig. 2b). However, the conclusion that habitat is discrete or continuous depends on the spatial scale being considered. The appropriate scale to assess discreteness of the habitat depends on the movements of individuals. Salmon could in principle travel between more or less distant locations and spawn in several of them during the same breeding season. Nevertheless, several studies have clearly shown that this is not the case: male sockeye salmon tend to remain in the same restricted area until they die. Observed movements of sockeye salmon were <100 m in a small tributary of Lake Aleknagik, Wood River (Stewart *et al.* 2004; Rich *et al.* 2006). Even more restricted were movements between two spawning grounds at Fuel Dump Island beaches in Iliamna Lake, separated by a section of 15 m of unoccupied habitat (Fig. 2c); in this case, the few males that moved had a very low reproductive success: from 0.003% to 3% of residents' success (Hendry *et al.* 1995). Only rarely (≪1%) do we observe a mature tagged salmon in more than one creek in the same breeding season (Thomas P. Quinn, unpublished data). The main reasons for limited male movements are probably the high costs associated with the establishment of new dominance relationships and the limited benefits when the density of ripe females is high. As a consequence of this limited tendency to move during the spawning season, even relatively short sections of unsuitable stream or beach seem to be sufficient to delimit distinct populations with few, if any, movements or interbreeding by adults among them in a given season. This situation is probably exacerbated in degraded areas, where suitable sections may be more isolated along rivers. Finally, the separation of individual groups in streams and lakes could be reinforced by differences in spawning period, creating temporal separation of populations called isolation by time (Hendry and Day 2005), or by preferences of individuals for certain habitat types (Lin 2007). In summary, a local population of salmon would typically breed in a stream or beach site, separated from other suitable sites by a distance such as that salmon might routinely move within this site but seldom move between sites.

Is there some asynchrony in the dynamics of local populations?

The second condition for the existence of metapopulation structures is that the dynamics of all local populations are not perfectly correlated, i.e. that some asynchrony exists (Fig. 1); otherwise, the persistence of the metapopulation is no greater than the persistence of any of the local populations. However, synchrony in the dynamics can result from at least two different processes (Liebhold *et al.* 2004 and references therein). On the one hand, populations that experience the same or similar environmental conditions often react in a similar way. On the other hand, dispersal among population also tends to synchronize populations when the number of immigrants is high enough compared to the population size of the receiving population.

Altogether, asynchrony of salmon local dynamics seems to be sufficient at each spatial scale to allow for metapopulation dynamics and to prevent the simultaneous extinction of a large number of populations. As an example, Peterman *et al.* (1998) found correlation coefficients below 0.75 for survival rates of sockeye salmon at the regional or larger scale (Fig. 3). This is confirmed by other studies, both at the regional scale: approximately −0.50 to 1.00 for distances up to 175 km in the Kvichak River system (Stewart *et al.* 2003a); and at the very local scale: approximately −0.35 to 0.095 for distances on the order of 1 km among spring-fed ponds near Pedro Bay, Iliamna Lake (Thomas P. Quinn, unpublished data).

Dispersal among populations seems to be too limited (see below) to play a role in synchronizing
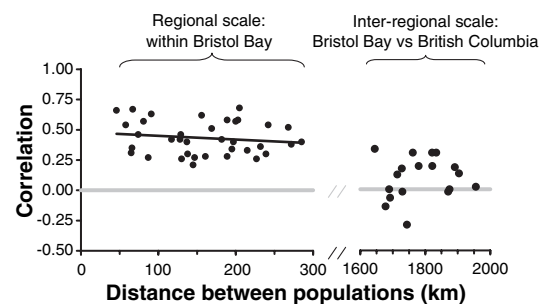

Figure 3 Condition 2: there is some asynchrony between local population dynamics. Correlation in local dynamics according to the distance between sockeye salmon populations (data from Peterman *et al.* 1998). Data at regional scale: correlation among the nine districts of Bristol Bay; at inter-regional scale: correlation between Bristol Bay and two populations in British Columbia (Nass and Skeena). The measure of local dynamics used to compute correlation was time series of brood year residuals from a Ricker stock-recruitment model (recruits per spawner as a negative exponential function of spawner abundance). Distances are given as straight line.

populations, except in situations when abundance decreases to low levels (Isaak *et al.* 2003) or perhaps for certain types of habitats, e.g. beaches (Stewart *et al.* 2003b). Some environmental conditions are clearly shared by several local populations at more or less large scales, e.g. fry spawned in different tributaries enter and rear in the same lake, and smolts from different lakes experience similar conditions in Bristol Bay and the North Pacific Ocean, and are likely to be responsible for some synchrony (Mueter *et al.* 2005; Pyper *et al.* 2005). Nevertheless, heterogeneity in habitat features and life history traits, collectively termed 'biocomplexity' (Hilborn *et al.* 2003), may induce a different response of the populations to the same cause (Kindvall 1996). For example, a drop in lake level during incubation might adversely affect all beach populations but streams and rivers might see lesser and more variable effects. Biocomplexity therefore counteracts the synchronizing effects of similar environmental conditions, and keeps levels of correlation well below 1.0 even for populations of the same region. This interaction with biocomplexity is probably also responsible for the fact that environmental conditions explain a relatively small proportion of the variability in salmon survival rates (Mueter *et al.* 2005), and that dynamics of Kvichak River sockeye populations spawning in similar habitats are more synchronized than those spawning in different habitat types (Stewart *et al.* 2003a).

Generally, both shared environmental conditions and dispersal are assumed *a priori* to be more likely to happen for populations close to each other; for many species correlation effectively decreases with the distance between populations (Liebhold *et al.* 2004). However, the decay of correlation with distance in sockeye salmon is extremely limited at the local and regional scales, while more important at a larger scale (Peterman *et al.* 1998; Stewart *et al.* 2003a; Fig. 3). One reason for such a pattern likely resides in the anadromous nature of salmon. Individuals from different populations of the same region, even very distant populations, meet in the same area during the time they spend at sea or are subject to processes that are well correlated over large spatial scales (Quinn 2005 and references therein). There, they encounter similar conditions affecting their survival, e.g. coastal conditions experienced by juvenile salmons and influenced by the Pacific Decadal Oscillation (Mantua *et al.* 1997; Mueter *et al.* 2005). In addition, common climate

factors, e.g. temperature and precipitation, might affect populations during their freshwater life history stages over large areas within years. Therefore, similar correlations are expected for populations of the same region, whatever the real distance between their spawning grounds is. Indeed, populations close to each other experience similar freshwater conditions, but all populations in a certain region experience similar, although certainly not identical, marine conditions. This breaks the 'closer populations experience more similar conditions' relation up to some spatial extent, while populations farther away, experiencing different freshwater and marine conditions, are less correlated or even negatively correlated if climate-driven processes such as upwelling create favourable conditions in part of the species' range and adverse conditions elsewhere (Mantua *et al.* 1997; Mueter *et al.* 2005).

What is the magnitude of dispersal between populations?

The third and critical determinant of metapopulation dynamics is the existence of dispersal between local populations (Fig. 1). In many terrestrial organisms, the magnitude of dispersal depends primarily on the distance between populations and is influenced by the existence of corridors or barriers in the landscape matrix and the mobility of the organisms. On the contrary, in anadromous species all fish start their return to spawn from the sea. Dispersal is therefore not really influenced by physical barriers: all populations are accessible; otherwise they would rapidly go extinct. While in theory each population might be reached by every individual, in practice dispersal is determined by the marine distribution of the populations and the homing fidelity of the fish, i.e. the tendency to return and spawn in the precise area where they were spawned. Consequently, a distance effect on dispersal rate of anadromous species may exist, probably not as a function of the Euclidian or nautical distance between populations but more of the number of splits in the streams between populations, each split being an occasion where the individual may stray while on the way to its natal population.

The homing tendency is very strong in salmon (Quinn 2005 and references therein) and the spatial scale to which they home can be extraordinarily precise (Quinn *et al.* 2006). Nevertheless, some

individuals stray and join another population for spawning, either by error in memory or orientation, or by choice to avoid adverse local conditions (Quinn 1993). In general, salmon tend to stray to rivers near their natal river, although not necessarily to the most proximate river containing conspecifics (Quinn and Fresh 1984; Quinn *et al.* 1991; Pascual and Quinn 1994). However, the frequency of such dispersal events and the relation with distance between populations are not well known, especially for wild populations, and vary greatly between species, regions and spatial scales (Quinn 1993; McElhany *et al.* 2000 and references therein; Jonsson *et al.* 2003). Despite considerable search in the literature and databases, we have been unable to find data on the frequency of dispersal events for Bristol Bay sockeye, as directly measured using capture–mark–recapture or other techniques; such data exists for other species, e.g. Atlantic (Jonsson *et al.* 2003; Consuegra *et al.* 2005; Consuegra and de Leaniz 2007) or pink salmon (*Oncorhynchus gorbuscha*, Salmonidae) (Thedinga *et al.* 2000). However, Beacham *et al.* (2005, 2006) collected a huge amount of data on genetic differentiation of sockeye salmon populations across the Pacific Rim, providing some insight into the scale and magnitude of gene flow (Fig. 4). Even if estimates of gene flow and dispersal obtained from figures of genetic differentiation, such as the number N_m of migrants per generation, should be taken with caution (Whitlock and McCauley 1999), these data clearly indicate that there is some dispersal between salmon

populations, and that this dispersal decreases with the distance between populations.

The fraction of strayers, or dispersers, even if quite low in general, seems largely sufficient to ensure (re)colonization of suitable habitat. Numerous examples of rapid natural recolonizations by salmonids have been observed in several species, e.g. after glacial recession in southeast Alaska (Quinn 1993; Milner *et al.* 2000) or after some natural or artificial barrier is removed (Bryant *et al.* 1999; Anderson and Quinn 2007). Even if a small fraction of strays seems at first glance incompatible with such a high power of (re)colonization, it is not. Indeed, given the large runs of many salmonid populations, a small fraction may easily represent several to tens of individuals. Such a number may be enough to colonize a vacant habitat and found a new population, because salmon are very productive when breeding at low densities and imprinting permits the fixation in a single generation of the new reproductive location (Quinn 2005 and references therein). At small distances, dispersal might also rescue small populations before extinction. Nevertheless, immigrants are probably seldom numerous enough to affect population dynamics in the target population, and especially to synchronize dynamics of source and target populations. The exception would be if the source and target populations differed vastly in abundance, e.g. a large hatchery and a small wild population (Nicholas and Van Dyke 1982) or if some factor induced elevated rates of straying, e.g. hatchery practices (Pascual
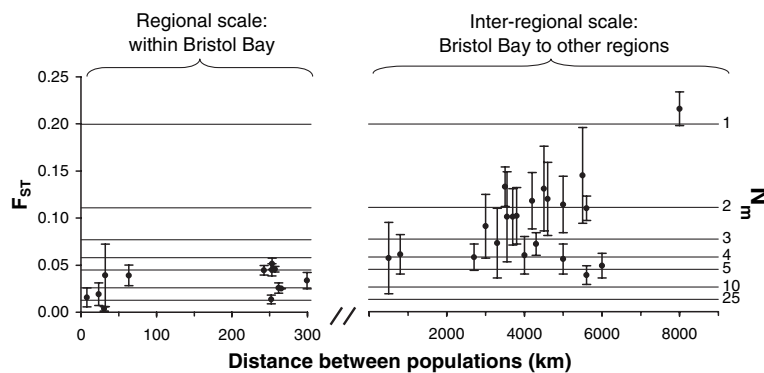

Figure 4 Condition 3: there is some dispersal between populations. Genetic differentiation according to the distance between sockeye salmon local populations: mean + SD of all pairwise F_{ST} values averaged over 14 microsatellite loci from 22 regional groups of sockeye salmon that were sampled at 299 locations across the Pacific Rim (data from Beacham *et al.* 2006 and T.D. Beacham, personal communication). Data at regional scale: within Bristol Bay (Iliamna, Aleknagik, Nerka and Clark lakes and Ruth river); at inter-regional scale: between Bristol Bay and the 21 other regional groups. Distances are given as straight line.

et al. 1995) or extreme natural conditions such as the 1980 eruption of Mt St Helens (Leider 1989). Dispersal that is low in proportion but high in number of individuals is responsible for rapid (re)colonization, leading the species to occupy all or nearly all suitable habitats is typical of salmon. This pattern, playing only a very limited role in synchronizing populations, is unusual in metapopulation dynamics. It may also explain why some species seem to be unable to colonize distant areas. For example, some anadromous salmonid species are native to only one coast of their respective ocean such as masu salmon (*Oncorhynchus masou*, Salmonidae) to the Asian side of the Pacific and cutthroat trout (*Oncorhynchus clarki*, Salmonidae) and bull trout (*Salvelinus confluentus*, Salmonidae) to the North American side, brown trout (*Salmo trutta*, Salmonidae) to the European side of the Atlantic Ocean and brook trout (*Salvelinus fontinalis*, Salmonidae) to the North American side. Presumably, suitable habitat in the other coast is so distant from the source populations and the marine migrations so limited that only one or at most a few immigrants arrive at a time. Even if they found a new population, it would be so distant from all other populations that its probability of extinction is relatively high. In such a scenario, these anadromous salmonids with limited marine migrations would present a high colonization power of areas on the edges of the occupied area, but a low colonization power in distant areas.

In addition to the spatial separation of populations, the patterns of age at maturity can result in some degree of temporal separation as well. At the extreme, pink salmon (*O. gorbuscha*, Salmonidae) mature at a fixed age of 2 years, virtually without exception (Heard 1991). This creates two temporally separated populations in some places, spawning on odd or even numbered years, of which only one exists in some areas (Heard 1991; Hard *et al.* 1996). Dispersal between odd and even year populations in a given spawning ground is caused by individuals maturing at an age different from two; the high degree of genetic separation between even and odd year lines in a river demonstrates the rarity of this event (Churikov and Gharrett 2002). In such a case, the previous discussion on the consequences of asynchrony and dispersal in space equally applies to asynchrony and dispersal in time, the variation between individuals in the age at reproduction determining the magnitude of temporal dispersal between populations. Other, less extreme,

cases include coho salmon (*Oncorhynchus kisutch*, Salmonidae), in which the great majority of females and many males mature at the same age (Sandercock 1991), and some populations of sockeye salmon that show strong cycles of abundance (Ricker 1950).

What is the variation in size and quality among habitat patches?

The variation in size and quality of the habitat (spawning ground) among populations may have important consequences for the functioning of the metapopulation. For salmon, a model with one or more 'mainlands', i.e. populations so big that their extinction is extremely improbable compared to other populations (Fig. 1), is not likely to correctly represent reality. Indeed, while differences in the sizes of the spawning grounds occupied by different populations affect their probability of extinction, even very large ones are not immune to extinction caused by catastrophes unrelated to population sizes. Cataclysmic events such as the 1980 eruption of Mt St Helens in Washington State, USA (Leider 1989) that totally devastate large populations are very infrequent, but there are more frequent but also more local events such as landslides and beaver dams that can affect or even eliminate not so small populations. On a more routine basis, differences in the quality of the spawning and rearing habitat greatly influence the number of recruits per spawner, i.e. the population growth rate, as well as density of spawners. Consequently, models with source and sink populations (Cooper and Mangel 1999) might be quite appropriate in some areas (Hindar *et al.* 2004). This might be especially true where the habitat has been degraded by human activities but high quality habitats are available nearby, for example in national parks or reserves.

Discussion and perspectives

Metapopulation structure for anadromous fish

Many anadromous fish species are likely to possess life history traits that are completely in agreement with the conditions for metapopulations to form and persist, as illustrated in this paper by the specific case of salmonids: a habitat fragmented into discrete patches, sufficient asynchrony in the dynamics of local populations, and dispersal events connecting populations. Nevertheless, anadromous fish meta-

populations are likely to present a mixture of features from different types of metapopulations, differing among spatial scales (Dunham and Rieman 1999), among regions depending on the habitat template and among species due to life history variations. Two aspects of salmon biology may especially influence the features of metapopulations. First, the broad geographical range of salmon encompasses many regions with very different geological histories and current conditions. For example, the east coast of Vancouver Island is relatively straight and so dispersal might occur primarily from/to nearest neighbour populations, and an 'isolation by distance' model might characterize relationships between populations. However, the west coast is deeply indented with a series of bays, and dispersal might be primarily within rather than between bays. Likewise, basins of large rivers (e.g. the Willamette and Yakima basins, on the west and east sides of the Cascade Mountains in the Columbia River) may also differ in features that affect dispersal of individuals and linkages of population dynamics. Second, life history traits of the different salmonids species may affect the extent of dispersal. The species vary in the duration of marine residence and the extent of migrations at sea (Quinn and Myers 2004) and this probably affects dispersal rates among regions. Indeed, the existence of non-anadromous forms of the species (e.g. kokanee – non-anadromous sockeye salmon: Wood 1995) or non-anadromous individuals of typically anadromous species (e.g. males in many populations of masu salmon: Kato 2007) likely affects the nature of (meta)population structure in these species.

In addition, human activities are likely to affect many aspects of salmonid metapopulation dynamics. In regions still close to their pristine state, like Bristol Bay, Alaska, the habitat supports many populations of sockeye salmon with thousands of spawning adults. Fisheries remove a large number and proportion of individuals, commonly 50–70% or more in recent years (Clark *et al.* 2006), but they are restricted to meet an escapement goal ensuring compensation by a relaxed competition for breeding space by adults and for food and space by juveniles (Minard and Meacham 1987; Hilborn *et al.* 2003). As a result of this large local abundance, population extinctions may be rare, and dispersal events frequent enough to rapidly recolonize vacant but suitable habitat. In such a case, all apparently suitable habitats are occupied, and metapopulation persistence is more a function of local population

persistence than a balance of extinctions and recolonizations. Such systems correspond more to patchy populations than to classical metapopulations (Fig. 1) but are not real patchy populations as the progeny from all populations are not completely mixed among habitat patches in each generation (Harrison and Taylor 1997). Anyway, in the longer term, metapopulation processes are likely to play a significant role in the persistence of viable salmonid populations because the habitat is dynamic, creating extinctions and opportunities for (re)colonizations. On the other hand, in human-dominated landscapes, the habitat is dynamic at short-time scales as well, owing to habitat modifications, and extinctions are more frequent (Nehlsen *et al.* 1991). Obviously, when the habitat is fully destroyed, populations go extinct deterministically and there is no potential for recolonization. However, in many places the habitat is simply altered to a state that sustains fewer individuals, e.g. road effect on bull trout (Dunham and Rieman 1999). The probability of stochastic extinction is greatly increased and extinctions may frequently and repeatedly occur, usually when an external negative event such as a drop in embryo survival rate because of drought or flood occurs. In this latter situation, the role of metapopulation dynamics in the persistence of the overall system is likely to be much more important; new populations must be founded at a sufficient rate to balance local extinctions. These may be natural recolonizations owing to individuals dispersing from other populations, or artificial reintroductions when individuals are moved to a restored habitat, e.g. after dam removal (Bryant *et al.* 1999). In such situations, it is important that conservation and management policies also protect vacant but suitable habitat because it provides the opportunity for the new populations necessary to compensate for extinctions in nearby populations (Young 1999). The simple conservation of currently occupied habitats may not be enough to ensure the long-term persistence of the metapopulation.

Priorities for future research

Metapopulation-based structures are likely for anadromous fish populations, but further research is needed to formally test for their existence. Equating the existence of dispersal with the reality of metapopulation dynamics, as often carried out in the literature, is not satisfactory from a rigorous scientific point of view. Furthermore, detailed studies are

needed to collect quantitative data for mathematical models of (meta)population functioning, for example for population viability analysis (Beissinger and McCullough 2002 and references therein; examples on salmonids: Nickelson and Lawson 1998; Legault 2005). Based on the processes leading to metapopulation dynamics (Fig. 1), several priorities may be delineated for further research.

1 Criteria must be defined for the delineation of suitable habitats that are based on features of the biotope and not on the presence of fish. This is a pre-requisite for the identification of suitable but vacant habitats, which can prove to be crucial for management and conservation. This implies determining the requirements of the species under study in terms of spawning and rearing habitat, and assessing where these requirements are met (Nickelson 1998; Burnett *et al.* 2007). This is not as simple as it might first seem. Many accessible streams with apparently suitable habitat are devoid of one or more species.

2 Asynchrony in local dynamics among populations is a key element of metapopulation dynamics. Several aspects must be studied in more detail on anadromous fish. First, specific methods must be used to estimate population growth rate (i.e. the ratio between abundances at time $t + 1$ and t, giving the number of recruits per spawner), because this is the basic demographic parameter on which to estimate correlation between populations, and because growth rate, and not local abundance, is the pertinent variable for detection of source and sink habitat patches and determination of features that are linked to habitat quality (Cooper and Mangel 1999; Dunham and Rieman 1999). Indeed, because of the mixing of generations in time, it is not trivial to compute the abundance of 'recruit' generation because it is spread over several years. Research aiming at improving these methods is a priority because inaccuracies in growth estimates can mask existing correlations among populations (Peterman *et al.* 1998). Furthermore, the collection of long-term data across numerous populations and different life stages, even if costly, is vital to the efficient application of these methods. Second, quantifying the variation in population asynchrony with distance among populations, and how it differs among species and depends on life history traits, including habitat selection, are other fields

where research is needed (Mueter *et al.* 2002; Stewart *et al.* 2003a). Quantifying asynchrony is necessary to assess the likelihood of correlated extinctions because of a common environmental event. Third, it is important to remember that correlation of local dynamics may be due to similar environmental conditions, to dispersal, or more likely to a combination or both. Methods that combine different types of information to partition the roles of these two processes in creating synchrony between populations are needed.

3 Several aspects of prime importance concerning dispersal are still poorly understood. It is advisable to focus research efforts on studying processes more than patterns. The first aspect to be studied in more detail is the spatial scale of dispersal movements; it must be assessed precisely to be able to delineate what constitutes a population. While many studies show that salmon are able to home to their natal ground with great precision (Quinn *et al.* 1999, 2006; Stewart *et al.* 2003b), the very spatial scale at which homing occurs in practice is still largely unknown for wild populations: is it just the lake, river or tributary, or is it even more precise? Studies of dispersal should determine origin and destination populations (Jonsson *et al.* 2003 for Atlantic salmon in Norway, and Pascual and Quinn 1994; Candy and Beacham 2000; Keefer *et al.* 2005 for Pacific salmon) rather than merely the proportion that strayed. Even more important, straying should not be presented merely as a negative process leading to the loss of fish. Dispersal can be studied using a variety of natural and induced marks and identifying features among populations. There is no lack of techniques, only a scarcity of application to the key questions (Quinn *et al.* 1999 and references therein), although there are often significant practical problems in marking large numbers or fractions of wild populations. Movements during the reproductive season may also contribute to dispersal and can be studied by marking and/or radiotelemetry. The second aspect where studies are needed concerns the reproductive success of dispersers. Indeed, whatever the movement is, its impact on (meta)population dynamics and gene flow depends on the successful breeding of the immigrant fish. If dispersers experience very low reproductive success, the effect of dispersal might be overestimated if only the dispersal rate

is taken into account (Hendry *et al.* 1995). The important aspect to study is therefore the effective dispersal, i.e. the number and reproductive success of dispersers that effectively reproduce in a population different from their natal population. Genetic studies might help in estimating these effective dispersal rates, but it is important to remember that it is rare that estimates of genetic variance among populations (e.g. F_{ST} values) can be translated into accurate estimates of number of dispersers (Whitlock and McCauley 1999).

Conclusion

This paper details why metapopulation-based structures are likely for many anadromous fish species. Metapopulation dynamics are, by definition, processes occurring on relatively large scales, often much larger that the territory covered by the jurisdiction of a specific management agency. This is particularly true for anadromous fish species because the series of biotopes they need for their different life stages are spread over large areas of land and ocean. Therefore, we urge all actors, people, institutions, states, etc., involved in the study, management and conservation of salmonids and other anadromous fish to develop collaborative studies and management actions at scales embracing the whole collection of sites needed for a viable metapopulation.

References

Anderson, J.H. and Quinn, T.P. (2007) Movements of adult coho salmon (*Oncorhynchus kisutch*) during colonization of newly accessible habitat. *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 1143–1154.

Baguette, M. (2004) The classical metapopulation theory and the real, natural world: a critical appraisal. *Basic and Applied Ecology* **5**, 213–224.

Beacham, T.D., Candy, J.R., McIntosh, B. *et al.* (2005) Estimation of stock composition and individual identification of sockeye salmon on a Pacific Rim basis using microsatellite and major histocompatibility complex variation. *Transactions of the American Fisheries Society* **134**, 1124–1146.

Beacham, T.D., McIntosh, B., MacConnachie, C., Miller, K.M. and Withler, R.E. (2006) Pacific rim population structure of Sockeye salmon as determined from microsatellite analysis. *Transactions of the American Fisheries Society* **135**, 174–187.

Beissinger, S.R. and McCullough, D.R. (2002) *Population Viability Analysis*. The University of Chicago Press, Chicago, IL, xvi + 577 pp.

Boorman, S.A. and Levitt, P.R. (1973) Group selection on the boundary of a stable population. *Theoretical Population Biology* **4**, 85–128.

Brown, J.H. and Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**, 445–449.

Bryant, M.D., Frenette, B.J. and McCurdy, S.J. (1999) Colonization of a watershed by anadromous salmonids following the installation of a fish ladder in Margaret Creek, Southeast Alaska. *North American Journal of Fisheries Management* **19**, 1129–1136.

Burnett, K.M., Reeves, G.H., Miller, D.J., Clarke, S., Vance-Borland, K. and Christiansen, K. (2007) Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. *Ecological Applications* **17**, 66–80.

Candy, J.R. and Beacham, T.D. (2000) Patterns of homing and straying in southern British Columbia coded-wire tagged chinook salmon (*Oncorhynchus tshawytscha*) populations. *Fisheries Research* **47**, 41–56.

Churikov, D. and Gharrett, A.J. (2002) Comparative phylogeography of the two pink salmon broodlines: an analysis based on a mitochondrial DNA genealogy. *Molecular Ecology* **11**, 1077–1101.

Clark, J.H., Mecum, R.D., McGregor, A., Krasnowski, P. and Carroll, A.M. (2006) The commercial salmon fishery in Alaska. *Alaska Fishery Research Bulletin* **12**, 1–146.

Clinchy, M., Haydon, D.T. and Smith, A.T. (2002) Pattern does not equal process: What does patch occupancy really tell us about metapopulation dynamics? *American Naturalist* **159**, 351–362.

Consuegra, S. and de Leaniz, C.G. (2007) Fluctuating sex ratios, but no sex-biased dispersal, in a promiscuous fish. *Evolutionary Ecology* **21**, 229–245.

Consuegra, S., Verspoor, E., Knox, D. and de Leaniz, C.G. (2005) Asymmetric gene flow and the evolutionary maintenance of genetic diversity in small, peripheral Atlantic salmon populations. *Conservation Genetics* **6**, 823–842.

Cooper, A.B. and Mangel, M. (1999) The dangers of ignoring metapopulation structure for the conservation of salmonids. *Fishery Bulletin* **97**, 213–226.

Cury, P. (1994) Obstinate nature – an ecology of individuals – thoughts on reproductive-behavior and biodiversity. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 1664–1673.

Dias, P.C. (1996) Sources and sinks in population biology. *Trends in Ecology and Evolution* **11**, 326–330.

Dunham, J.B. and Rieman, B.E. (1999) Metapopulation structure of bull trout: Influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications* **9**, 642–655.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* **34**, 487–515.

Fraser, D.J. and Bernatchez, L. (2001) Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Molecular Ecology* **10**, 2741–2752.

Fromentin, J.M. and Powers, J.E. (2005) Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. *Fish and Fisheries* **6**, 281–306.

Garant, D., Dodson, J.J. and Bernatchez, L. (2000) Ecological determinants and temporal stability of the within-river population structure in Atlantic salmon (*Salmo salar* L.). *Molecular Ecology* **9**, 615–628.

Gende, S.M., Edwards, R.T., Willson, M.F. and Wipfli, M.S. (2002) Pacific salmon in aquatic and terrestrial ecosystems. *BioScience* **52**, 917–928.

Gilpin, M. and Hanski, I. (1991) *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, London.

Gotelli, N.J. and Taylor, C.M. (1999) Testing metapopulation models with stream-fish assemblages. *Evolutionary Ecology Research* **1**, 835–845.

Gowan, C. and Fausch, K.D. (1996) Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. *Ecological Applications* **6**, 931–946.

Hanski, I. (1989) Metapopulation dynamics: does it help to have more of the same? *Trends in Ecology and Evolution* **4**, 113–114.

Hanski, I. (1998) Metapopulation dynamics. *Nature* **396**, 41–49.

Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford, 313 pp.

Hanski, I. (2002) Metapopulations of animals in highly fragmented landscapes and population viability analysis. In: *Population Viability Analysis* (eds S.R. Beissinger and D.R. McCullough). The University of Chicago Press, Chicago, pp. 86–108.

Hanski, I. and Gaggiotti, O.E. (2004) *Ecology, genetics, and evolution of metapopulations*. Academic Press, Amsterdam, 696 pp.

Hanski, I. and Gilpin, M.E. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**, 3–16.

Hanski, I. and Gilpin, M.E. (1997) *Metapopulation Biology, Ecology, Genetics, and Evolution*. Academic Press, San Diego, 512 pp.

Hanski, I. and Simberloff, D.S. (1997) The metapopulation approach, its history, conceptual domain, and application to conservation. In: *Metapopulation Biology, Ecology, Genetics and Evolution* (eds I. Hanski and M.E. Gilpin). Academic Press, San Diego, pp. 5–26.

Hanski, I., Pakkala, T., Kuussaari, M. and Lei, G.C. (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos* **72**, 21–28.

Hard, J.J., Kope, R.G., Grant, W.S., Waknitz, F.W., Parker, L.T. and Waples, R.S. (1996) *Status Review of Pink Salmon from Washington, Oregon, and California*. National Marine Fisheries Service, Tech. Memo. NMFS-NWFSC-25, Seattle, WA.

Harrison, S. (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* **42**, 73–88.

Harrison, S. (1994) Metapopulation and conservation. In: *Large-Scale Ecology and Conservation Biology* (eds P.J. Edwards, R.M. May and N.R. Webb). Blackwell, Oxford, pp. 111–128.

Harrison, S. and Taylor, A.D. (1997) Empirical evidence for metapopulation dynamics. In: *Metapopulation Biology, Ecology, Genetics and Evolution* (eds I. Hanski and M.E. Gilpin). Academic Press, San Diego, pp. 27–42.

Heard, W.R. (1991) Life history of pink salmon (*Oncorhynchus gorbuscha*). In: *Pacific Salmon Life Histories* (eds C. Groot and L. Margolis). University of British Columbia Press, Vancouver, BC, pp. 119–230.

Hendry, A.P. and Day, T. (2005) Population structure attributable to reproductive time: isolation by time and adaptation by time. *Molecular Ecology* **14**, 901–916.

Hendry, A.P., Leonetti, F.E. and Quinn, T.P. (1995) Spatial and temporal isolating mechanisms – the formation of discrete breeding aggregations of sockeye-salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology* **73**, 339–352.

Hilborn, R. and Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty*. Chapman and Hall, New York, NY, 570 pp.

Hilborn, R., Quinn, T.P., Schindler, D.E. and Rogers, D.E. (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 6564–6568.

Hill, M.F., Hastings, A. and Botsford, L.W. (2002) The effects of small dispersal rates on extinction times in structured metapopulation models. *American Naturalist* **160**, 389–402.

Hindar, K., Tufto, J., Saettem, L.M. and Balstad, T. (2004) Conservation of genetic variation in harvested salmon populations. *Ices Journal of Marine Science* **61**, 1389–1397.

Isaak, D.J., Thurow, R.F., Rieman, B.E. and Dunham, J.B. (2003) Temporal variation in synchrony among chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 840–848.

Jager, H.I., Chandler, J.A., Lepla, K.B. and Van Winkle, W. (2001) A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. *Environmental Biology of Fishes* **60**, 347–361.

Jonsson, B., Jonsson, N. and Hansen, L.P. (2003) Atlantic salmon straying from the River Imsa. *Journal of Fish Biology* **62**, 641–657.

Kato, F. (2007) Life histories of masu and amago salmon (*Oncorhynchus masou* and *Oncorhynchus rhodurus*). In: *Pacific Salmon Life Histories* (eds C. Groot and L. Margolis). University of British Columbia Press, Vancouver, pp. 448–520.

Keefer, M.L., Peery, C.A., Firehammer, J. and Moser, M.L. (2005) *Straying rate of know-origin adult chinook salmon and steelhead within the Columbia River Basin, 2000–2003*. Technical Report 2005-5, University of Idaho, http://www.cnr.uidaho.edu/uiferl/pdf%20reports/05-5%20straying%20AMS%2025Aug05.pdf (accessed on 09/01/2007).

Kindvall, O. (1996) Habitat heterogeneity and survival in a bush cricket metapopulation. *Ecology* **77**, 207–214.

Koizumi, I. and Maekawa, K. (2004) Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. *Freshwater Biology* **49**, 973–981.

Kritzer, J.P. and Sale, P.F. (2004) Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries* **5**, 131–140.

Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**, 911–927.

Legault, C.M. (2005) Population viability analysis of Atlantic salmon in Maine, USA. *Transactions of the American Fisheries Society* **134**, 549–562.

Leider, S.A. (1989) Increased straying by adult steelhead trout, *Salmo gairdneri*, following the 1980 eruption of Mount St. Helens. *Environmental Biology of Fishes* **24**, 219–229.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**, 237–240.

Levins, R. (1970) Extinction. In: *Some Mathematical Questions in Biology. Lectures on Mathematics in the Life Sciences*, volume 2 (ed. M. Gerstenhaber). American Mathematical Society, Providence, Rhode Island, pp. 77–107.

Liebhold, A., Koenig, W.D. and Bjornstad, O.N. (2004) Spatial synchrony in population dynamics. *Annual Review of Ecology Evolution and Systematics* **35**, 467–490.

Lin, J. (2007) *Genetic Divergence among Distinct Phenotypes of Sockeye Salmon (Oncorhynchus nerka)*. MSc thesis, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. and Francis, R.C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* **78**, 1069–1079.

McElhany, P., Ruckelshaus, M., Ford, M.J., Wainwright, T.C. and Bjorkstedt, E.P. (2000) *Viable salmonid populations and the recovery of evolutionarily significant units*. NOAA Technical Memorandum NMFS-NWFSC – 42, US Department of Commerce, 156 pp.

Milner, A.M., Knudsen, E.E., Soiseth, C., Robertson, A.L., Schell, D., Phillips, I.T. and Magnusson, K. (2000) Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 2319–2335.

Minard, R.E. and Meacham, C.P. (1987) Sockeye salmon (*Oncorhynchus nerka*) management in Bristol Bay, Alaska. *Canadian Special Publication of Fisheries and Aquatic Sciences* **96**, 336–342.

Mueter, F.J., Ware, D.M. and Peterman, R.M. (2002) Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the north-east Pacific Ocean. *Fisheries Oceanography* **11**, 205–218.

Mueter, F.J., Pyper, B.J. and Peterman, R.M. (2005) Relationships between coastal ocean conditions and survival rates of northeast Pacific salmon at multiple lags. *Transactions of the American Fisheries Society* **134**, 105–119.

Naiman, R.J., Bilby, R.E., Schindler, D.E. and Helfield, J.M. (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* **5**, 399–417.

National Research Council (1996) *Upstream: Salmon and Society in the Pacific Northwest*. Committee on Protection and Management of Pacific Northwest Anadromous Salmonids, National Academy of Science, Washington, DC, 472 pp.

Nehlsen, W., Williams, J.E. and Lichatowich, J.A. (1991) Pacific salmon at the crossroads – stocks at risk from

California, Oregon, Idaho, and Washington. *Fisheries* **16**, 4–21.

Nicholas, J.W. and Van Dyke, L. (1982) *Straying of Adult Coho Salmon to and from a Private Hatchery at Yaquina Bay, Oregon.* Oregon Department of Fish & Wildlife (USA) Information Report 82-10. 16 pp.

Nickelson, T.E. (1998) *A Habitat-Based Assessment of Coho Salmon Production Potential and Spawner Escapement Needs for Oregon Coastal Streams.* Oregon Department of Fish and Wildlife, Information Report 98-4, Portland, OR.

Nickelson, T.E. and Lawson, P.W. (1998) Population viability of coho salmon, *Oncorhynchus kisutch*, in Oregon coastal basins: application of a habitat-based life cycle model. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2383–2392.

Pascual, M.A. and Quinn, T.P. (1994) Geographical patterns of straying of fall chinook salmon (*Oncorhynchus tshawytscha*) from Columbia River (USA) hatcheries. *Aquaculture and Fisheries Management* **25**, 17–30.

Pascual, M.A., Quinn, T.P. and Fuss, H. (1995) Factors affecting the homing of Columbia River hatchery-produced fall chinook salmon. *Transactions of the American Fisheries Society* **24**, 308–320.

Peterman, R.M., Pyper, B.J., Lapointe, M.F., Adkison, M.D. and Walters, C.J. (1998) Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2503–2517.

Pimm, S.L. and Raven, P. (2000) Biodiversity – extinction by numbers. *Nature* **403**, 843–845.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist* **132**, 652–661.

Pyper, B.J., Mueter, F.J. and Peterman, R.M. (2005) Across-species comparisons of spatial scales of environmental effects on survival rates of Northeast Pacific salmon. *Transactions of the American Fisheries Society* **134**, 86–104.

Quinn, T.P. (1993) A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research* **18**, 29–44.

Quinn, T.P. (2005) *The Behavior and Ecology of Pacific Salmon and Trout.* University of Washington Press, Seattle, WA, 320 pp.

Quinn, T.P. and Fresh, K.L. (1984) Homing and straying in chinook salmon (*Oncorhynchus tshawytscha*) from Cowlitz River Hatchery, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 1078–1082.

Quinn, T.P. and Myers, K.W. (2004) Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. *Reviews in Fish Biology and Fisheries* **14**, 421–442.

Quinn, T.P., Nemeth, R.S. and McIsaac, D.O. (1991) Homing and straying patterns of fall chinook salmon in the lower Columbia River. *Transactions of the American Fisheries Society* **120**, 151–156.

Quinn, T.P., Volk, E.C. and Hendry, A.P. (1999) Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology* **77**, 766–775.

Quinn, T.P., Stewart, I.J. and Boatright, C.P. (2006) Experimental evidence of homing to site of incubation by mature sockeye salmon, *Oncorhynchus nerka.* *Animal Behaviour* **72**, 941–949.

Rich, W.H. (1939) Local populations and migration in relation to the conservation of Pacific salmon in the western states and Alaska. In: *The Migration and Conservation of Salmon* (ed F.R. Moulton). Publ. Am. Assoc. Advanc. Sci., No. 8). Lancaster, PA, pp. 45–50.

Rich, H.B.J., Carlson, S.M., Chasco, B.M., Briggs, K.C. and Quinn, T.P. (2006) Movements of male sockeye salmon, *Oncorhynchus nerka,* on spawning grounds: the effects of in-stream residency, density, and body size. *Animal Behaviour* **71**, 971–981.

Ricker, W.E. (1950) Cycle dominance among the Fraser sockeye. *Ecology* **31**, 6–26.

Ricker, W.E. (1972) Hereditary and environmental factors affecting certain salmonid populations. In: *The Stock Concept in Pacific Salmon* (eds R.C. Simon and P.A. Larkin). H. R. MacMillan Lectures in Fisheries, University of British Columbia Press, Vancouver, BC, pp. 19–160.

Rieman, B.E. and Dunham, J.B. (2000) Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. *Ecology of Freshwater Fish* **9**, 51–64.

Sandercock, F.K. (1991) Life history of coho salmon (*Oncorhynchus kisutch*). In: *Pacific Salmon Life Histories* (eds C. Groot and L. Margolis). University of British Columbia Press, Vancouver, pp. 395–445.

Schaefer, J.A. (2006) Towards maturation of the population concept. *Oikos* **112**, 236–240.

Schtickzelle, N. and Baguette, M. (2004) Metapopulation viability analysis of the bog fritillary butterfly using RAMAS/GIS. *Oikos* **104**, 277–290.

Schtickzelle, N., Mennechez, G. and Baguette, M. (2006) Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* **87**, 1057–1065.

Smedbol, R.K., McPherson, A., Hansen, M.M. and Kenchington, E. (2002) Myths and moderation in marine 'metapopulations'? *Fish and Fisheries* **3**, 20–35.

Stacey, P.B., Johnson, V.A. and Taper, M.L. (1997) Migration within metapopulations – the impact upon local population dynamics. In: *Metapopulation Biology, Ecology, Genetics and Evolution* (eds I. Hanski and M.E. Gilpin). Academic Press, San Diego, CA, pp. 267–291.

Stamps, J.A., Krishnan, V.V. and Reid, M.L. (2005) Search costs and habitat selection by dispersers. *Ecology* **86**, 510–518.

Stewart, I.J., Hilborn, R. and Quinn, T.P. (2003a) Coherence of observed adult sockeye salmon abundance within

and among spawning habitats in the Kvichak river watershed. *Alaska Fishery Research Bulletin* **10**, 28–41.

Stewart, I.J., Quinn, T.P. and Bentzen, P. (2003b) Evidence for fine-scale natal homing among island beach spawning sockeye salmon, *Oncorhynchus nerka*. *Environmental Biology of Fishes* **67**, 77–85.

Stewart, I.J., Carlson, S.M., Boatright, C.P., Buck, G.B. and Quinn, T.P. (2004) Site fidelity of spawning sockeye salmon (*Oncorhynchus nerka* W.) in the presence and absence of olfactory cues. *Ecology of Freshwater Fish* **13**, 104–110.

Taylor, P.D., Fahrig, L., Henein, K. and Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos* **68**, 571–573.

Thedinga, J.F., Wertheimer, A.C., Heintz, R.A., Maselko, J.M. and Rice, S.D. (2000) Effects of stock, coded-wire tagging, and transplant on straying of pink salmon (*Oncorhynchus gorbuscha*) in southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 2076–2085.

Thomas, C.D. and Hanski, I. (1997) Butterfly metapopulations. In: *Metapopulation Biology, Ecology, Genetics and Evolution* (eds I. Hanski and M.E. Gilpin). Academic Press, San Diego, CA, pp. 359–386.

Tilman, D., May, R.M., Lehman, C.L. and Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature* **371**, 65–66.

Van Dyck, H. and Baguette, M. (2005) Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology* **6**, 535–545.

Waples, R.S. (1991) *Definition of ''Species'' under the Endangered Species Act: Application to Pacific Salmon.* NOAA Technical Memorandum NMFS F/NWC-194. US Department of Commerce, Washington, DC, 29 pp.

Whitlock, M.C. and McCauley, D.E. (1999) Indirect measures of gene flow and migration: F-ST not equal 1/(4Nm + 1). *Heredity* **82**, 117–125.

Wiens, J.A. (2001) The landscape context of dispersal. In: *Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhondt and J.D. Nichols). Oxford University Press, New York, pp. 96–109.

Wilcove, D., Rothstein, D., Dubow, J., Phillips, A. and Losos, E. (1998) Quantifying threats to imperiled species in the United States. *BioScience* **48**, 607–615.

Willson, M.F. and Halupka, K.C. (1995) Anadromous fish as keystone species in vertebrate communities. *Conservation Biology* **9**, 489–497.

Wood, C.C. (1995) Life history variation and population structure in sockeye salmon. *American Fisheries Society Symposium* **17**, 195–216.

Young, K.A. (1999) Managing the decline of Pacific salmon: metapopulation theory and artificial recolonization as ecological mitigation. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1700–1706.