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The ecology of recovery

Anna Gårdmark[1], Katja Enberg[2]*, Jörgen Ripa[2,1], Jouni Laakso[2] &
Veijo Kaitala[2,3]

[1] *Department of Theoretical Ecology, Lund university, Ecology building, SE-223 62 Lund, Sweden*
[2] *Integrative Ecology Unit, Division of Population Biology, University of Helsinki, P.O. Box 65, FIN-00014 University of Helsinki, Finland (*e-mail: katja.enberg@helsinki.fi)*
[3] *Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40351 Jyväskylä, Finland*

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The current high rate of population declines and attempts to 'manage' their recovery, call for a better understanding of recovery dynamics of populations. In many cases, recovery of a population may primarily be determined by a single life history property or ecological interaction, allowing for straightforward management actions. For example, a generalist predator may prevent the recovery of its prey, and populations with sex-biased dispersal are particularly vulnerable to demographic stochasticity. However, linking life history with intra- and interspecific population dynamics is needed to assess the relative importance of these factors. A clear example is depensatory dynamics that can be caused either by e.g., mutual predation or cooperative breeding. Moreover, dynamics of a recovering population can alter both its physiological and behavioural traits, affecting its interspecific interactions. Here we review life histories (reproduction, resource use and dispersal) and species interactions affecting recovery processes, and discuss their implications for management.

Introduction

All populations are likely to either have experienced or will come to experience major crashes in population numbers due to natural population fluctuations (caused by unstable inherent dynamics, unstable interactions with other species, or by demographic stochasticity) or due to natural or man-induced environmental changes. Often these crashes are followed by recoveries, as evidenced by historical bottlenecks as in the northern elephant seal (*Mirounga angustirostris*; Weber *et al*. 2000). Sometimes, however, the recovery of a population may fail. With the current high rate of population declines, mainly due to human activities (Vitousek *et al*. 1997), there is an urgent need to understand the factors limiting and facilitating population recoveries. This is particularly important for the attempts to 'manage' recoveries, for example, by habitat restoration, breeding programs and reintroductions.

There is a growing interest for the factors governing the recovery dynamics of populations (e.g., Hutchings 2000, Kareiva 2002), and the best means to manage such recoveries (Kareiva 2002 and references therein). Population recovery is determined both by ecological and evolutionary processes. Here, we discuss how the life history of a species and its interactions with other species govern its probability and rate of recovery.

The influence of evolutionary processes on population recovery is dealt with in e.g., Schlaepfer *et al*. (2002). An analysis of the factors promoting and inhibiting the recovery of a population by necessity includes an assessment of all the cases of non-recoveries, that is, extinctions. These are, however, dealt with elsewhere in this issue (e.g. Benton 2003).

The definition of population recovery requires a notion of the temporal dynamics of the population. For this paper we define recovery as the re-growth of a population after a decline to exceptional densities (of one order of magnitude less than pre decline population size) or (local) extinction. Thus, here we do not treat the effect of life histories and species interactions on population dynamics in general, but primarily on the dynamics of populations at low densities, which we call recovery dynamics.

Rate of recovery

The time necessary for a population to recover to pre-disturbance densities is determined by its growth rate. At low densities the population growth is determined by its intrinsic (i.e., density-independent) rate of increase, whereas at higher densities the population growth rate decreases due to the competition with conspecifics over limited resources. The population then grows according to its (density-dependent) population growth rate. Species with a high intrinsic growth rate will thus have a higher probability and, initially, a higher rate of recovering than species with a lower intrinsic growth rate.

A number of factors determine population growth rate. Traits such as age-at-maturation determine the intrinsic growth rate (Myers & Mertz 1997), and strategies of reproduction and feeding determine both intrinsic growth rate and mechanisms of intraspecific density-dependence. Stochastic variation in environmental conditions generally decreases population growth rate (Tuljapurkar & Cashwell 1997). Whether environmental stochasticity can seriously impair population growth is determined by the interaction between life history properties and the environmental stochasticity. For example, stochastic growth rate in plants with seed bank may be very little affected by large variance in recruitment rates, whereas plants with weak seed storage suffer from variability in recruitment (for a review *see* Higgins *et al*. 2000). In practise this also means that organisms with strong storage may appear declining for a long time but nevertheless recover in a very unpredictable manner.

Since no species live in isolation, growth rate of a population also depends on densities of other species that it interacts with. Thus, even at low densities, the intrinsic growth rate of a population is not the sole factor governing the rate of its recovery. In competitive communities, for example, species that strongly (negatively) depend on densities of interacting species take a longer time to recover from low density than species with the same intrinsic growth rate but weaker dependence on densities of non-conspecifics (Gårdmark, A., Enberg, K. & Lundberg, P., unpubl.). However, strong competition does not always imply slow recovery in stochastic environments. Competing species may periodically recover from low density when disturbance changes the competitive ranking or opens up free space, which results in coexistence (Sale 1977, Levins 1979, Chesson & Warner 1981).

Life histories and population recovery

Characterisation of the life histories of species with fast versus slow population dynamics was prompted by the prediction of how life histories would evolve in different environments — the theory of *r*- and *K*-selection by MacArthur & Wilson (1967). The fast dynamic species (*r*-selected) are predicted to be small, have fast body growth, mature early and have high fecundity, whereas the slow dynamic ones (*K*-selected) are large, late maturing species with slow body growth and low fecundity (Pianka 1970). Few studies, however, have proved such connections from data. Sæther *et al*. (2002) only recently showed that the pattern of population fluctuations of solitary bird species could be coupled to their life history characteristics. In populations with slow dynamics, the dynamics were primarily driven by adult survival, whereas those with fast population dynamics were recruitment-driven. Below we discuss how strategies of reproduction, resource use and dispersal influence the dynamics of recovering populations and present some of the few examples where the effect of life history on population dynamics have been documented.

Reproduction

Reproduction strategies influence population growth rate in several ways. Especially important for population recovery is reproduction at low population densities. If low densities entail difficulties in finding partners to mate with, per capita reproduction decreases with declining densities (below some threshold density). Population growth rate is then positively density-dependent at low densities, which is known as the Allee effect (Odum 1959) or depensatory dynamics. A population that falls below this threshold cannot recover since it will have negative growth rate. Mechanisms leading to decreased per capita rate of increase at low densities have been demonstrated in many species (Courchamp *et al.* 1999a, Stephens & Sutherland 1999), although evidence for depensatory dynamics from population-level data is ambiguous (Myers *et al.* 1995, Liermann & Hilborn 1997). However, some species showing impeded recovery from exploitation also show Allee effects in reproduction (e.g., the Caribbean queen conch *Strombus gigas*; Stoner & Ray-Culp 2000).

The most common explanation for depensatory dynamics is low rate of encounters with conspecifics when rare, shown to decrease population growth rate in, for example, the endangered Glanville fritillary butterfly (*Melitaea cinxia*; Kuusaari *et al.* 1998). Related to this is lek-breeding that occurs across taxa (e.g., fallow deer (*Dama dama*), black grouse (*Tetrao tetrix*) and frogs), where a minimum number of (usually) males displaying in the same area is required for females to attend (Höglund 1996). However, there are several other mechanisms that cause depensatory dynamics. In corporate breeders reproducing individuals rely on helpers to feed young, and if group size decreases juvenile mortality increases (e.g., in suricates; Clutton-Brock *et al.* 1999). Juvenile survival may also increase even without active facilitation, due to the particular environmental conditions created in large colonies, as in for example social spiders (*Anelosimus eximius*; Aviles & Tufino 1998). The presence of other individuals can also help defer predators, either through predator vigilance (as in bird colonies), active defence by attack (e.g., in colonial male bluegill sunfish, *Lepomis macrochirus*; Côté & Gross 1993) or by confusion behaviours (such as schooling in fish), or dilution (i.e., the probability for an individual to be attacked decreases with group size).

Small populations are sensitive to stochastic effects, and especially so if not all mature individuals reproduce. Populations with a skewed operational sex ratio (i.e., the proportion of individuals that reproduces differ between the sexes; Emlen & Oring 1977) can have difficulties in recovering from low population sizes since only few individuals of one sex attempt to breed. Skewed operational sex ratios, common in many taxa (e.g., *Hymenoptera*, spiders, frogs, reptiles, birds and mammals), occur due to harem holding, when few individuals of one sex monopolise matings, or due to facultative adjustment of offspring sex ratios in response to changing environments (Charnov 1982, Sheldon 1998, Byholm *et al.* 2002). The skewed sex ratio in, for example, Yellow perch *Perca flavescens* (inflicted by sex-biased fishing) in Lake Michigan contributed to its prolonged period of low recruitment when recovering from overfishing (Madenjian *et al.* 2002).

Resource use

The selection and mode of resource use of a species obviously influences its recovery dynamics. When a particular resource decreases, species specialised on that resource take longer to recover than generalist species, which can switch to other resources (shown in, for example, ground-beetles recovering from logging; Niemelä *et al.* 1993). Although a species may be a generalist with respect to its choice of food resources, the way it obtains resources can make it a specialist with respect to, for example habitat requirements; reducing their probability of recovering from habitat disturbance. For example, in the Australian snake family *Elapidae* there are two strategies of prey capture: by ambush (relying on sites with particular types of ground cover) or active search. A phylogenetic comparison showed that the endangered species in the family were ambush predators — due to lack of recovery after human habitat disturbance — whereas the non-endangered ones actively searched for prey (Reed & Shine 2002).

Differences in resource use *within* a population can cause recovery rate to be influenced by the age-, size-, sex- or stage-structure of the population. For example, in species with ontogenetic niche shift, age (or size) groups may grow differently following a disturbance because they use different food resources. Another possible cause is that individuals may differ in their ability to reuse resources. One example is the recovery of the lady beetle *Epilachna niponica* following flooding (Ohgushi 1996). In this species, females recovered much more rapidly than males because of their ability to reallocate energy from reproduction to survival, through egg resorption. The change in different age-, size-, or sex-groups determines the growth rate of the population as a whole (Caswell 2000), and differential resource use within a population is therefore crucial for recovery.

The effect of differences in resource use on population dynamics is even more pronounced in cannibalistic populations where one size group feeds on another (occurring in e.g., insects (Dodds *et al*. 2001), amphibians (Wakano *et al*. 2002), and fish (Persson *et al*. 2000)). Cannibalism may permit a population to recover because it enables the population to persist under food conditions when an otherwise identical non-cannibalistic one would go extinct. However, since cannibalistic populations often show alternative stable states (e.g., Fisher 1987, Cushing 1992), once at a smaller (but persistent) population size, further population growth is hindered. Most work on population dynamical effects of cannibalism is theoretical (reviewed in Claessen 2002), but cannibalism has been shown to influence recruitment dynamics of, for example, Eurasian perch *Perca fluviatilis* (Persson *et al*. 2000) and Baltic cod *Gadus morhua* (Jarre-Teichmann *et al*. 2000).

Dispersal

A locally extinct population can recover only if it is re-colonised by immigrants from other populations. This can occur either by individuals moving to the empty habitat, or by extending their home ranges from neighbouring habitats (shown to be the main factor behind recovery in e.g., Australian brushtail possums (*Trichosurus vulpecula*) (Ji *et al*. 2001)). Rebuilding of local populations is crucial also for the recovery and persistence of metapopulations (Stacey *et al*. 1997). For recovering slow-growing populations a flow of immigrants may be more important than local population renewal to alleviate the vulnerability to stochastic effects in reproduction when the population is small (*see* also the 'Managing recoveries' section below).

Spiller *et al*. (1998) studied small island populations right before and after as well as one year after a hurricane. The results clearly show the importance of dispersal ability, as the poorer dispersers (lizards) did not recover whereas better dispersers (web spiders) showed clear recovery (Spiller *et al*. 1998). The type of dispersal strategy influences a population's recovery. The distance of dispersal is obviously important (for example, for forest recoveries in abandoned agricultural land; Cubina & Mitchell 2001), but also whether dispersal is density-dependent or age-, size-, or sex-specific. When dispersal is sex-biased, as for example in birds where natal dispersal is female-biased (Dale 2001), remote populations do not only suffer from low immigration rate but may also obtain a highly skewed sex ratio, which further may hamper recovery. The importance of dispersal for a species' ability to recover depends on the relative importance of other survival strategies in changing environments (e.g., Valbuena & Trabaud 2001). An alternative to spatial redistribution is to disperse in time, i.e., to store reproductive propagules (e.g., in seed banks) or to minimise energy-consuming activities through diapause (that is, hibernation or in lower animals, e.g., cryptobiosis). For example, recovery of plant communities after disturbance often relies heavily on seed banks (Del Castillo 1994, Ferrandis *et al*. 1996).

Dispersal may not only rebuild local populations but also decrease local population size if emigration is high. If emigration is positively density-dependent, as for example in territorial species, there is little emigration when the population is small, and the population can therefore recover more easily. However, in some species emigration rates have shown to be negatively density-dependent (e.g., the Glanville frittillary butterfly (Kuusaari *et al*. 1998) and Australian rabbit *Oryctolagus cuniculus* populations (Richardson *et al*. 2001)), resulting in depensatory dynamics and failure to recover if population size drops below some critical threshold.

Recovery effects on life-history characteristics

Life-history characteristics influence recovery dynamics of populations, but the reverse is also true: population dynamics can crucially determine important life-history traits, since many traits are density-dependent. For example, populations recovering from previous exploitation will contain individuals of smaller size-at-age than when exploited, due to density-dependent body growth (Fabrizio *et al*. 2001; A. Gårdmark *et al*. unpubl.), common in, for example, exploited fish populations (Lorenzen & Enberg 2002). The classical 'maternal effects' hypothesis of rodent population cycles provides another example of how a recent decline may affect population life-history characteristics. Individuals in a declining phase of a cycle can be in such bad condition due to overcrowding, stress from predators and/or depleted resources that their reproduction is reduced. The maternal effects hypothesis proposes that this low fecundity is transferred to the offspring (a maternal effect), affecting the dynamics of the population, which could explain the extended low phase and delayed recovery of some cyclic rodents (Chitty 1952, Mihok & Boonstra 1992). There is some empirical support for this theory (Mihok & Boonstra 1992), but recent field experiments by T. Klemola and co-workers contradict that maternal effects influence population dynamics. Field voles (*Microtus agrestis*) from different phases of a cycle grow in numbers equally fast once all predators are removed (Klemola *et al*. 2002). The reason may be that in field voles, as in many organisms with cyclic or outbreak-type dynamics, the generation length is short compared to the period length of the cycle. Therefore, although changes in population density affect fecundity, it is unlikely that maternal effects play a major role in preventing population recovery in these organisms.

Density increases during population recovery can induce changes also in non-physiological traits, such as food choice. Following liming of an acidified lake in Norway the brown trout (*Salmo trutta*) and its prey the Arctic char (*Salvelinus alpinus*) both increased in density in the late 1980s. Due to density-dependent somatic growth the average size-at-age of char decreased to sizes that were within the capturable range for the brown trout. The trout then became piscivorous, feeding on the char. Due to the higher energy content in fish than plankton, this reappearance of an ontogenetic niche shift allowed the trout to grow in body size more rapidly, to sizes not recorded since the early 1970s (Andersen & Vollestad 1996). Thus, life-history characteristics and the dynamics of recovering populations are crucially interdependent, and their interrelationship can even affect interactions between species, with further repercussions for population recovery dynamics.

Species interactions and population recovery

Recovery of a population can be either hampered or facilitated by the presence of other species, depending on the type of interactions between them. In the most straightforward case, the population decline and recovery are caused by the same interaction. This is exemplified in classical predator–prey cycles, where the decline and subsequent recovery are in principle endlessly repeated. In these, recovery of the prey population is possible because the predator (or parasite or consumer) population lags behind the prey (or host or resource) population. Once the predator catches up, the prey crashes to low densities, and it will not recover until the predator has declined as well. Classic examples of cyclic dynamics are the Northern rodents (Hanski & Henttonen 1996, Stenseth *et al*. 1996) and their specialist predators, and the snowshoe hare–lynx cycle

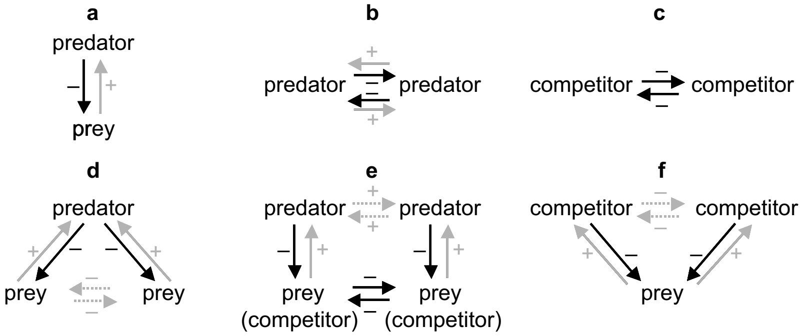

Fig. 1. Short-term (black) and long-term (grey) direct (full lines) and indirect (dotted lines) interactions between species occurring in (**a**) predation, (**b**) mutual predation, (**c**) interference competition, (**d**) apparent competition, (**e**) an example of indirect facilitation, and (**f**) resource competition.

(Elton 1924). Most studies of vole cycles have however concentrated on the causes of population collapse and relatively few on the increase phase. Recent analyses of natural time series and field experiments nevertheless suggest that the recovery of a cyclic prey or host from low phase is due to a release from predator or parasite pressure (e.g., Hanski & Henttonen 1996, Stenseth *et al*. 1996, Hudson *et al*. 1998, Korpimäki & Nordahl 1998, Klemola *et al*. 2000, 2002).

Population cycles are an example of the simple case when a particular interaction, such as predation, is the direct cause of a population decline and subsequently the crucial factor for the (lack of) recovery. Non-cyclic examples of the same general scenario involve many kinds of interactions and are easily found in the literature. A more complicated situation, and perhaps more interesting, emerges when the recovery of a population is heavily dependent on an interaction that was not directly responsible for the previous decline. Below we explain and exemplify such effects of two-species and multi-species interactions, illustrating important direct and indirect effects of species interactions on recovery dynamics.

Two-species interactions

Predation (Fig. 1a) causes extra mortality on prey populations and therefore slows down the rate of, or even halts, recovery of the prey population. For example, fur seals (*Arctocephalus gazella*) have been shown to recover from exploitation at a lower rate in populations predated by lion seals (*Hydrurga leptonyx*; Boveng *et al*. 1998). In some of the populations predation is so intense that recovery has stopped altogether and they decline. Failure to recover has also been attributed to predation in economically important exploited fish populations. For example, the Northeast Atlantic cod (*Gadus morhua*) stocks that collapsed in 1992 are believed to be kept from recovering by predation from grey seal (*Halichoerus grypus*; Fu *et al*. 2001), or harp seals (*Phoca groenlandica*; Bundy 2001).

Similar to predation, parasitism can also reduce the rate of recovery by increasing mortality or decreasing reproduction. For example, the recovery of several fish populations (lake whitefish (*Coregonus clupeaformis*), burbot (*Lota lota*) and to some extent salmonides) from overfishing and eutrophication in Lake Michigan was greatly improved by control of sea lamprey (*Petromyzon marinus*; Madenjian *et al*. 2002), which is an ectoparasite on fish. Release from parasite load is also considered a major cause of recovery in many insect populations, a process which may be economically important when the insect species is a pest (e.g., Maron *et al*. 2000, Hicks *et al*. 2001, Hertz & Heitland 1999).

The other end of a predator–prey or host–parasite interaction is the effect of the prey on the recovery of the consumer, which needs a viable resource population to recover. Provided that the predator population decreases due to a factor unrelated to the prey population, the prey population is released from predation and can rapidly reach higher abundances. This allows the predator to grow rapidly once the extrinsic factor causing the predator decline is removed. However, if the predator population declines due to overexploitation of the prey, recovery of the predator population will be delayed, occurring only after the prey population is rebuilt.

A more complicated predatory interaction emerges when two species both are each other's predators and preys, that is, when there is mutual predation (Fig. 1b). The species then both benefit and are disadvantaged by each other's presence. If one of them is reduced to low density by an external factor, the other species is released from predation and can increase. The rare species is then strongly controlled by predation, which may hinder its recovery. Both species thus show depensatory dynamics, and the system can shift between two alternative stable states, causing the disturbed species to be 'trapped' at low density. One example of mutual predation is between populations of cod (*Gadus morhua*) and herring species (*Clupea harengus*), where herring feeds on cod eggs and larvae, and cod feeds on small herrings (Sparholt 1994). This has been used to explain the recovery dynamics of cod in the Gulf of St. Lawrence. Following collapse in the mid 1970s the cod recovered rapidly whereas it has not recovered since the crash in 1992. The first collapse coincided with very low abundances of herring, whereas currently the herring is increasing together with all-time high abundances of other pelagic cod-predating species (Swain & Sinclair 2000).

Competition with other species also reduces the rate of population recovery. For example, during recovery from wintertime ice scorching in a rocky shore community, the brown seaweed *Fucus* slowed down the rate of population growth in barnacles (*Semibalanus balanoides*) and ephemeral algae (e.g., *Hildenbrandia rubra*) due to its higher competitiveness for space (McCook & Chapman 1997). The effect of a species on its competitor depends on whether they compete directly or indirectly. That is, if competition occurs by direct interference between the species (Fig. 1c), or if it is resource competition (Fig. 1f), i.e., when the two competitors interact indirectly via a shared prey species. The effect of the latter, indirect, interaction is slower than the direct, since an increase in the competing species is tangible for its competitor only after it has reduced the common prey population.

Two competing species may also be affected to a different extent by the competition, if competition is asymmetric. This is important not only for the recovery dynamics of the two competitors, but in the case of resource competition (Fig. 1f), also for the recovery of their shared prey. Eiders (*Somateria mollissima*) and whelks (*Nucella lapillus*), for example, both feed on blue mussels (*Mytilus edulis*) in intertidal communities. The eider is the dominant competitor and has a great effect on the whelk population, but is itself little affected by whelks. Exclusion of eiders preventing their predation on the mussels caused an increase in the whelk population, whose predation prevented any population growth in mussels (Hamilton 2000). However, this interaction is somewhat more complicated: eider predation also facilitates whelk predation, by keeping the average size of mussels within the manageable consumption size of whelks. This crucially determined the recovery dynamics of the three species following experimental physical disturbance of the mussel population. In the absence of eider predation mussels rapidly grew to sizes larger than that preferred by whelks, due to compensatory somatic growth. However, if allowed, eiders started feeding on mussels before the population had rebounded, which allowed also for some whelk predation, and thus slowing the rate of mussel population recovery (Hamilton 2000). Thus, although the species are overall competitors, the facilitation of one species by the other hampered the recovery of their shared prey.

That two species that interact can do so in more than one way has important consequences for their recovery. One example is the two sea urchins *Diadema antillarum* and *Echinometra viridis* living on Caribbean coral reefs, which have shown to be competitors in addition/removal experiments (Williams 1981). However, following mass mortality of *D. antillarum*, its recruitment to coral reefs was *enhanced* by the alleged competitor *E. viridis*, even more so than by the presence of conspecifics (Lessios 1995). This is because grazing on algae by adult echinoids cues larval settlement, and the heavier grazing by *E. viridis* provided a stronger settlement cue (Lessios 1995). Recovery of *D. antillarum* is thus both facilitated by *E. viridis* (through increased settlement) and, once settled, impeded by competition.

Species that facilitate the recovery of another species can do so either mutually (mutualism) or one-directionally (commensalism). For example, following a catastrophic decline in the fig *Ficus aurea* due to a hurricane in Florida, its mutualistic pollinator the wasp *Pegoscapus jimenezi* was believed to be locally extinct. However, in only five months both the wasp and the amount of flowering fig had recovered to levels close to those prior to disturbance (Bronstein & Hossaert 1995). One example of commensalism facilitating recovery is the red sea urchins (*Strongylocentrotus franciscanus*) providing important shelter for juvenile abalones (*Haliotis* spp.) from crab predation. In urchin populations recovered from exploitation along the Californian coast more juvenile abalones were found, thus facilitating recovery of the abalone population, as compared to in exploited areas (Rogers-Bennett & Pearse 2001). Facilitating interactions, however, are often not direct interactions between the two species, but instead indirect interactions via changes in the quality of the habitat or resources, that is, via a third species.

Multi-species interactions

Two species that indirectly interact with each other via a third (or several other) species can either benefit or disadvantage each other. One example is the interaction between two predators feeding on two different prey species, which in turn compete with each other (Fig. 1e). Predation by one of them decreases the competitor to the food source of the other, thus benefiting the other predator population. This interaction has been shown to occur between brown hares (*Lepus europaeus*) and brent geese (*Branta bernicla*) in salt marshes (van der Wal *et al*. 2000). Winter grazing by hares suppresses the spread of a shrub, allowing for better growth of grass (the geese food source) and thus facilitating geese population growth.

Two species may also interact via a shared predator, a situation known as apparent competition (Fig. 1d). A prey species may then face difficulties to recover from low density since its predator population is sustained by its alternative prey. This hampers especially the growth of the preferred prey, since the predator will switch back to feeding on it once it starts to increase in density. Similarly, there may also be apparent competition between species due to a shared parasite, as for example between the ring-necked pheasant (*Phasianus colchicus*) and the grey partridge (*Perdix perdix*). The pheasant is less affected by the nematode parasite *Heterakis gallinarum* and thereby provides a source for maintaining infections of the partridge, causing its decline in the United Kingdom (Tompkins *et al*. 2002).

Interactions among species in more intricate food webs can be highly complex, involving several of the simpler interactions described above. Particularly important for population recoveries are when there are loops of interactions, such that the effects of one species on another is mediated via many other interactions to feed back on the first species, situations where there may often be alternative stable states. One example is the diverse and complex interactions among species associated with marine kelp (*Laminariales* spp.) ecosystems. One loop of interactions involves fish such as sheephead (*Semicossyphus pulcher*) and spiny lobster (*Panulirus interruptus*) that feed on urchins (*Strongylocentrotus* spp.). These urchins, in turn, feed on kelp, which provides habitat and food for the fish (Tegner & Dayton 2000). If the fish populations are brought to low abundances, they may be stuck in this alternative state due to the overgrazing of their feeding habitat (the kelp) caused by the increasing number of urchins that have been released from predation. Thus, once in an alternative state the community might be ‘closed’.

Managing recoveries

Managing recoveries may seem intuitively simple: we only have to remove the factor that caused the population decline. In all sections above we have given examples of aspects that affect recovery ability. Nevertheless, in many cases it is difficult to find the factor(s) that has triggered the population decline. For example, as we have showed in the Multi-species interactions chapter above, complex interrelations among species may obscure the ultimate cause of the decline. Knowledge of the factors governing population recovery is important also for management of non-recoveries, that is, within biological pest control (*see* e.g., 'Two-species interactions' chapter). In this chapter, we will give some examples of both successfully managed recoveries and failed ones and discuss the factors that have affected the outcome of recovery management attempts.

There are several examples of when merely removing the cause of the population decline has led to successful population recovery. Many seed-eating and raptor species declined severely in the 1960s when alkyl-mercury pesticides were used (Borg *et al*. 1969). The replacement of these chemicals with other pesticides (with the banning of organochlorines, such as PCB) contributed to population recoveries (Newton 1998). In harvested populations declining population sizes are relatively common phenomena, and decreasing the harvest pressure is a logical management effort. A successfully managed recovery of an overharvested population is the recovery of Norwegian spring spawning herring (*Clupea harengus*) stock, depleted in the beginning of the 1970s. A fishing moratorium (Bjørndal *et al*. 2000) enabled the recovery of the stock to levels sufficient for opening the fishery again.

Habitat restoration

The fact that habitat destruction is a common cause of population decline makes habitat restoration a natural management action. Successful habitat restorations can be found for e.g. fish (Raat 2001, Prignon *et al*. 1999) birds (Melvin *et al*. 1999), insects (Thomas & Jones 1993) and mammals (Richter *et al*. 1993). Sometimes mere protection of the habitat is enough — as in the case of endemic bird species Rodrigues fody on Mascarene Islands of Rodrigues (*Foudia flavicans*, Impey *et al*. 2002).

Restoration of whole lake ecosystems has been tried in the Netherlands but with limited success (*see* extensive review by Gulati & van Donk 2002). High influx of nutrients has eutrophicated many shallow lakes in the Netherlands, with ensuing high turbidity (due to cyanobacterial blooms) and loss of macroalgae. A mere reduction of the inflow of nutrients (phosphorus) does not seem sufficient to return the lakes to their former state, although there are some indications of recovery after a full two decades of nutrient reduction (Gulati & van Donk 2002). To speed up the process, Gulati & van Donk (2002) suggest various biomanipulation actions, despite ambiguous success in the past.

Reintroductions

There is a difference between restoring a partly destroyed habitat of an existing population and restoring a habitat of a population that has gone locally extinct. Recovery in the latter case requires a successful colonisation, which may or may not be facilitated by management actions. Restored habitat patches may be too isolated to receive enough immigrants for a recolonisation to take place within reasonable time. To determine when natural recolonisation is insufficient is often difficult, since dispersal ability varies greatly between species or even within species (Krohne & Hoch 1999). Artificial dispersal, or reintroduction, has been successfully tried for e.g. European beaver (*Castor fiber*; Halley & Rosell 2002) and greater prairie chicken (*Tympanus cupido pinnatus*; Westemeier *et al*. 1998). Another bird species that has benefited from relocation is the Chatman Island black robin (*Petroica travensi*), even though in this case also egg-manipulations and cross-fostering under another species were used (Butler & Merton 1992). Captive breeding, even though it may be considered as a last-chance management procedure, has helped many species including California condor (*Gymnogyps californiacus*; Collar *et al*. 1988) and Mauritius kestrel (*Falco punctatus*; Jones *et al*. 1995). Other examples of successfully recovered bird species can be found in Newton 1998.

In contrast to the success stories mentioned above, management procedures such as reintroductions may also fail, e.g., due to limited knowledge of the life history and interspecific interactions of the species. The attempt to reintroduce some orchid species to Great Britain appears to be, at least partly, unsuccessful (McKendrick 1995, Ramsay & Stewart 1998). The reason for this failure is the neglect of interspecific interactions: herbivory has been observed to be a major cause for jeopardizing the attempts of re-planting at the original sites of the plants. In addition, many orchid species need mycorrhiza symbiosis in order to survive and reproduce, although not much is known about the effects of the symbiotic relationships for re-introduction of the endangered species. Thus, in many situations consideration of other than the target species is crucial.

From a metapopulation point of view, a full recovery implies re-colonisation of several habitat patches until the former proportion of occupied patches is reached. Such a process can take a very long time (Thomas & Jones 1993), especially if colonisation rates only just exceed extinction rates (Ovaskainen & Hanski 2002). Also, networks with many small and close patches recover faster than networks with a few large, isolated patches (Ovaskainen & Hanski 2002). Nevertheless, the recolonisation process can be facilitated by reintroduction into strategic patches, located in different sub-networks of relatively connected patches, or the creation of stepping-stone habitats between such isolated networks of patches (Thomas & Jones 1993).

Complex interactions

Intricate interspecific interactions may substantially complicate recovery management attempts. Courchamp *et al.* (1999b) studied the effect of removing an introduced superpredator (feral cat) threatening endemic bird species in a system including also a mesopredator, introduced rat. Results showed that presence of only one predator may be sufficient to drive the endemic prey species to extinction, but also that removal of superpredator (cat) may ‘release’ the mesopredator (rat) which then may drive the endemic prey to extinction (Courchamp *et al.* 1999b). Another example of the importance of indirect species interactions is the lack of recovery of the Canadian Atlantic cod (*Gadus morhua*). In spite of fisheries moratoria population sizes have remained low (Frank & Brickman 2001). The lack of recovery is believed to be a consequence of seal predation (references in Swain & Sinclair 2000). However, seals also feed on other pelagic fish, which, in turn, feed on cod eggs and larvae. Therefore, decreasing the seal population size may not lead to recovery of the cod (Swain & Sinclair 2000). Predator removals have generally also failed to increase the breeding population size of threatened bird species. A meta-analysis of 20 attempts revealed that even though hatching success and post-breeding population size were most strongly affected by the management, the breeding population did not increase significantly, and the desired recovery did not occur. This was in most cases due to density-dependent winter mortality (affecting especially juveniles) or limited breeding habitat (Côté & Sutherland 1997). Successful example of predator removal comes from the island of Rarotonga, Cook Islands, where the monarch flycatcher (*Pomarea dimidiata*) recovered after almost a century of low population size: in a few years after an intensive predator (rat) control program, the flycatcher population doubled (Robertson *et al.* 1994).

As long as our understanding of the actual causes of a successful or unsuccessful recovery is relatively poor, it may be extremely difficult or even impossible to define which management action to take in a particular recovery management attempt, and seemingly straightforward management actions, for example, predator removal, may fail. The above examples show the main message of this chapter: successful management of recovery is possible (and can sometimes be achieved by merely removing the factor causing the population decline), but requires detailed knowledge of the life history and interspecific interactions of the target population.

Concluding remarks

In this review, we have exemplified aspects of life histories and species interactions that are important for the recovery of a population. One perhaps trivial conclusion is that ‘the ecology of recoveries’ is not different from any other ecology — the ecological processes that affect population growth under normal circumstances are still potentially important after a severe decline, the exception being of course intraspecific competition. However, in addition to these, there are some processes that are particularly important for recovering populations: those increasing vulnerability to demographic stochasticity, or causing depensatory dynamics, alternative stable states and compensatory responses.

Another conclusion is that finding the most important factor for the recovery of a population may be difficult, since there can be multiple causes involved. Studies discriminating these are scarce, especially comparisons of the significance of a species' traits and of its interactions with other species for its ability to recover. To advance the understanding of the factors governing population recoveries we need to link life history theory with population dynamics into comparative population dynamics, assessing the relative importance of intra- and interspecific processes for population dynamics. A failure to recover is thus possibly caused by a complex pattern of direct and indirect effects working at different spatial and temporal scales. However, we find such a conclusion premature and overly pessimistic. In the majority of cases we have discussed here there is a single life history property or ecological interaction determining the recovery of the focal population. Thus, the ecology of recoveries is not necessarily complex, but ecologists need to be open-minded about what kind of life-history trait or interspecific interaction could be the most important in any particular case.

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