

Depensation: evidence, models and implications

Martin Liermann¹ & Ray Hilborn²

¹Quantitative Ecology and Resource Management, University of Washington, Seattle, WA 98115, USA; ²School of Fisheries Box 355020, University of Washington, Seattle, WA 98195, USA

Abstract

We review the evidence supporting depensation, describe models of two depensatory mechanisms and how they can be included in population dynamics models and discuss the implications of depensation. The evidence for depensation can be grouped into four mechanisms: reduced probability of fertilisation, impaired group dynamics, conditioning of the environment and predator saturation. Examples of these mechanisms come from a broad range of species including fishes, arthropods, birds, mammals and plants. Despite the large number of studies supporting depensatory mechanisms, there is very little evidence of depensation that is strong enough to be important in a population's dynamics. However, because factors such as demographic and environmental variability make depensatory population dynamics difficult to detect, this lack of evidence should not be interpreted as evidence that depensatory dynamics are rare and unimportant. The majority of depensatory models are based on reduced probability of fertilisation and predator saturation. We review the models of these mechanisms and different ways they can be incorporated in population dynamics models. Finally, we discuss how depensation may affect optimal harvesting, pest control and population viability analysis.

Key words Allee effect, depensation, inverse density dependence

Correspondence:

Martin Liermann,
National Marine
Fisheries Service,
North-west Fisheries
Science Center, 2725
Montlake Blvd. E.,
Seattle, WA 98112–
2013, USA
Tel: +206 860 6781
Fax: +206 860 3335
E-mail: martin.
liermann@noaa.gov

Received 22 Sep 2000
Accepted 29 Nov 2000

Introduction	34
Definitions	34
Evidence for depensatory mechanisms	35
Reduced probability of fertilisation	36
Impaired group dynamics	37
Conditioning of the environment	39
Predator saturation	40
Difficulty detecting depensatory population dynamics	42
Modelling depensatory mechanisms	42
Reduced fertilisation success	43
<i>Accounting for individual differences in the encounter rate</i>	44
<i>Depletion of potential mates</i>	45
<i>Multiple matings</i>	45

Predator saturation	45
<i>Type I functional response curves</i>	45
<i>Type II functional response curves</i>	46
<i>Type III functional response curves</i>	46
<i>Incorporating the number of predators into the functional response curve</i>	47
<i>Accounting for prey depletion over time</i>	47
Population models that include depensation	49
The Ricker and Beverton–Holt SR models	49
Modifying the differential equation	50
Turning parameters into functions	50
Modelling multiple life history stages	51
Depensatory and compensatory effects dependent on the same life history stage	51
Model choice	53
Implications of depensation	53
Acknowledgements	54
References	54

Introduction

Many natural populations have been reduced to a small proportion of their historic levels (Scarff 1977a, 1977b; Nehlsen *et al.* 1991; Hutchings and Myers 1994). This has resulted in listings under the US Endangered Species Act and more cautious management of exploited populations (e.g. Magnuson-Stevens Act). Traditional models of population growth assume that reducing the density will always result in the same or higher per-capita growth. This implies that populations are resilient, allowing them to recover rapidly when the factors that caused their decline are removed (e.g. fishing or degraded habitat). However, when reduced to very low densities, some populations experience reduced rates of survival and reproduction (e.g. Allee 1938; Wood 1987; Fowler and Baker 1991). In these populations, recovery from low densities may be significantly delayed or not occur at all. This reduced per-capita growth rate at low densities is called depensation. The increased effects of demographic stochasticity at low densities and the fact that many populations rarely dip to these levels makes depensation very difficult to detect. To assess the possibility of depensation and its potential effects on a population, knowledge of when and how depensation occurs in other populations (of the same or different species) is important.

For populations that may exhibit depensation, mathematical models that include depensation are

necessary to predict how these populations will change under different management prescriptions and different assumptions about depensation. A familiarity with the different types of depensatory models provides a basis from which a model for a particular population can be chosen or adapted.

This review has six sections: (i) definitions of concepts that are related to depensation; (ii) a review of the evidence for depensatory mechanisms; (iii) a discussion of efforts to detect depensation from demographic data and potential reasons they have failed; (iv) a review of models of depensation; (v) methods of incorporating depensatory models into full population dynamics models; and (vi) some implications of depensation. While a great proportion of the literature on depensation is concerned with fish and fisheries, understanding depensation is facilitated if we explore the range of data available throughout ecology.

Definitions

There are a myriad of different terms and definitions that have been applied to the phenomena of depensation over the last 80 years. We describe the standard usage of depensation, list the many other names that have been used for the phenomena, and review the related terminology.

A population's dynamics are depensatory (or depensation is said to occur) if the per-capita rate of growth decreases as the density or abundance decreases to low levels. Components of the life-

history (such as fecundity or survival during a particular stage) or the mechanisms that affect these components (such as group defense or mate-finding difficulty) are called depensatory if they decrease the per-capita growth rate as density or abundance declines to low levels. Because other nondepensatory factors are also acting on the per-capita growth rate, a depensatory life-history component or mechanism does not translate directly into population dynamics that are depensatory. For example, increased per-capita availability of resources at low densities might more than make up for reduced effectiveness of group defenses. To avoid ambiguity, it is therefore important to distinguish between depensation (depensatory population dynamics) and a depensatory mechanism or life history component that may lead to depensation (Stephens *et al.* 1999).

Other names for depensation include: the Allee effect (after one of the first innovators in the field), the Allee–Robertson effect (acknowledging an even earlier contributor), allelocatalysis (after Robertson 1921), undercrowding (Andrewartha and Birch 1954), inverse density dependence (e.g. Courchamp *et al.* 1999), and negative density dependence (e.g. McCarthy 1997), negative competition (Stamou and Asikidis 1989), and cooperation (used in a very general sense by Jacobs 1984). The term depensation was first used to describe this phenomenon by Neave (1953). Depensation is the label most often used in fisheries, whereas the Allee effect is more common in the general biological literature. The opposite phenomenon has been labelled: compensation (Neave 1953); density dependence, overcrowding (Andrewartha and Birch 1954), and disoperation (Odum and Allee 1954). The term density dependence implies a more general concept that encompasses

depensation. Although it is occasionally used in this more general way (DeAngelis *et al.* 1977), it is predominantly used to denote only a negative effect of increased density on per-capita growth (see for example Sinclair 1989) (hence the use of inverse or negative density dependence to describe depensation).

Populations with depensatory dynamics may have negative per-capita growth at low densities. This has been called critical depensation (Clark 1985). The threshold or critical density (Clark 1985) at which the per-capita growth rate becomes negative is of particular interest since populations reduced below this density face decline, possibly to extinction (Fig. 1).

In some populations, depensation may lead to more complex dynamics. For example, when a population experiences predation that produces highest per-capita mortality at intermediate population levels, the population may have two stable equilibria (Fig. 2). If the population declines to the lower stable equilibrium it is said to be trapped in the predator-pit (Peterman 1977; Steele and Henderson 1984).

Evidence for depensatory mechanisms

Many mechanisms can lead to depensation (Allee 1938; Fowler and Baker 1991; Courchamp *et al.* 1999). These mechanisms have been categorised in several different ways (Allee *et al.* 1949; Andrewartha and Birch 1954; Jacobs 1984). Roughly following the conventions of previous authors, we have organised the evidence in this review according to four mechanisms: reduced probability of fertilisation, impaired group dynamics, conditioning of the environment and predator saturation.

Figure 1 When plotting per-capita growth as a function of population density, depensation produces a positive slope.

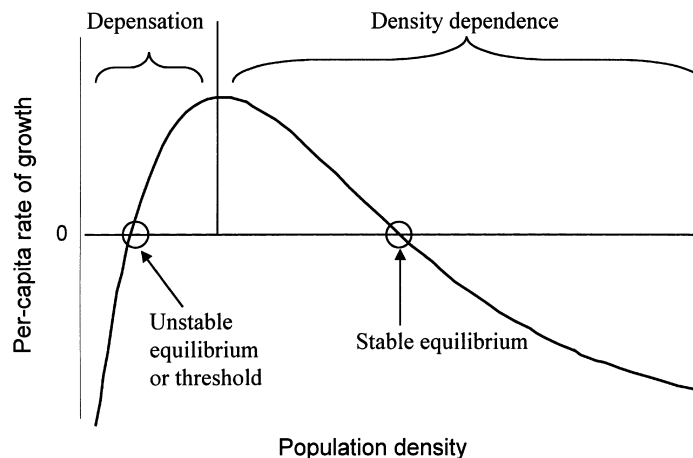
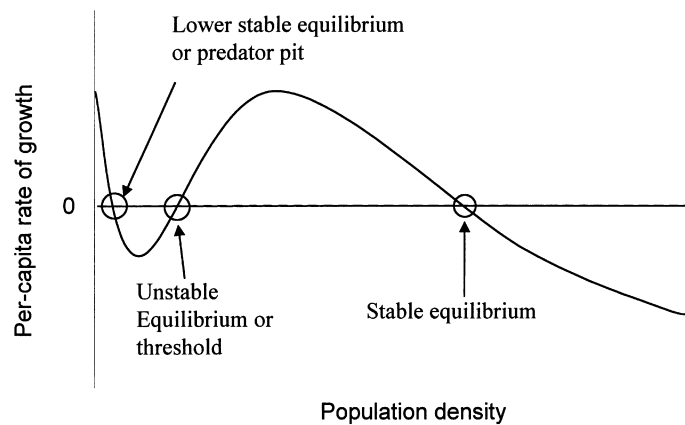


Figure 2 Two stable equilibria can result when a population is exposed to predation that has its strongest per-capita effect at intermediate densities.



The evidence in these sections support individual depensatory mechanisms that may or may not lead to depensatory population dynamics. Some of the evidence demonstrates depensation through a stage in the life history, while other evidence only supports the mechanism without showing a change in survival or fecundity.

Reduced probability of fertilisation

Reduced fertilisation success at low population densities can result from a number of different mechanisms (Table 1). One of the most commonly cited examples is difficulty in finding a mate (Errington 1940; Milne 1950; Kuussaari *et al.* 1998). As the density of a population decreases, the extra energy and time spent looking for a mate may reduce the overall reproductive success. Errington (1940) attributed reduced reproduction

at low densities in muskrats (*Ondatra zibethicus*, Muridae) to this mechanism. He found that breeding success was noticeably lower for populations with densities below approximately one pair per mile of stream. In organisms where individuals only have access to a small proportion of the potential mates (due to limited mobility or a fragmented population) difficulty in finding a mate is accentuated. When the sheep tick (*Ixodes ricinus*, Ixodidae) is ready to feed and mate, it crawls to the end of a grass stem and attaches to any sheep that happens to brush against it. At low tick densities, there is a reduced probability of finding another tick to mate with on the same sheep. This may explain a number of observations in which apparently suitable pastures remained free of ticks for decades, although they were adjacent to infested pastures (separated only by a fence). Milne (1950) hypothesised that as long as infected sheep

Table 1 A summary of the evidence for reduced probability of fertilisation at low densities.

Description	Source
Muskrats (<i>Ondatra zibethicus</i>) Breeding success was noticeably lower for populations with density below one pair per mile of stream	Errington (1940)
Sheep tick (<i>Ixodes ricinus</i>) Uninfected fields separated by a fence from infested fields only became infested when infested sheep were introduced to the uninfested fields	Milne (1950)
Glanville fritillary butterfly (<i>Melitaea cinxia</i>) 'Fraction of mated females decreases with decreasing local density'	Kuussaari <i>et al.</i> (1998)
Sea urchins The fertilisation rate was lower for the less densely spaced 'simulated' sea urchins	Levitan <i>et al.</i> (1992)
Plant (<i>Diplotaxis eruroides</i>), Australian tree (<i>Banksia goodii</i>), annual plant (<i>Clarkia concinna</i>) Fewer seeds produced in populations that are smaller and more isolated	Kunin (1992) Lamont (1993) Groom (1998)
Grey-tailed vole (<i>Microtus canicaudus</i>) Individuals avoid mating with familiar members of the population	Boyd and Blaustein (1985)

(carrying large numbers of the ticks) were not allowed onto the clean fields, depensation due to difficulty in mate finding would preclude an infestation. Even in organisms that are more mobile, mate finding can be a problem. In a study of the Glanville fritillary butterfly (*melitaea cinxia*, Nymphalidae), Kuussaari *et al.* (1998) showed that the 'emigration rate increases and the fraction of mated females decreases with decreasing local density.' They demonstrated that this translates to a reduction in reproductive success at lower densities.

In many sessile aquatic organisms, gametes from one or both sexes are released into the water and chance encounter between female and male gametes determines fertilisation. If the organisms are widely spaced, the gametes will also tend to be less dense, resulting in a lower probability of a chance encounter. Allee (1938) suggested that this mechanism should occur in sea urchins, but provided no experimental evidence. To test this hypothesis, Levitan *et al.* (1992) simulated spawning sea urchins spaced 0.5 and 2 meters apart, using sperm filled syringes as stand ins for male urchins and sperm permeable containers containing eggs to represent plumes of female gametes in the water column. To approximate natural conditions as closely as possible, the different density arrays of simulated urchins were placed in water 9 meters deep off the west coast of Vancouver Island in Canada. The fertilisation rate was lower for the less densely spaced urchins and for the treatments with fewer individuals (controlled for density), supporting Allee's assertion. These results suggest that many other species relying on this form of spawning may be affected by depensation at low densities.

Plants face similar reproductive difficulties at low densities. Smaller populations may be less likely to attract pollinators, and pollen from within these populations may be lower quality because the plants are more closely related. In a study of the Australian tree *Banksia goodii* (Proteaceae), Lamont *et al.* (1993) suggested that these mechanisms may be responsible for lower seed densities in the canopies of smaller populations. Larger distances between individual plants or patches of plants may also lead to reduced production of seeds (Kunin 1992; Groom 1998). In a study of the annual plant *Clarkia concinna* (Onagraceae), Groom (1998) found both 'pollen receipt and seed set were negatively related to isolation distance but positively related to patch size'. In addition, she noted that for small patches there appeared to be an isolation distance

threshold beyond which the pollen receipt and seed production dropped sharply.

In some species of small mammals, individuals avoid mating with familiar members of the population. Working with the grey-tailed vole (*Microtus canicaudus*, Muridae), Boyd and Blaustein (1985) found that voles reared together produced fewer litters than those reared apart even when those reared together had different parents. Based on these results they reasoned that 'in the field, familiarity of voles may increase in low density populations and reproductive behaviour may decline as a result.'

Impaired group dynamics

Beneficial group dynamics may be interrupted when population size is reduced (Table 2). For example, reproductive success is often reduced in smaller colonies of group nesting birds (Allee *et al.* 1949; Andrewartha and Birch 1954; Birkhead 1977; Raveling 1989; Emslie *et al.* 1995). One possible explanation is that in smaller colonies a larger proportion of the individuals are on the edge where chick predation has been shown to be higher. In Antarctica, Emslie *et al.* (1995) observed approximately 4–8 times more frequent predation and attempted predation on penguin chicks at the edge of colonies compared to the centre. They attributed the lower breeding success in smaller colonies at least in part to predation. Higher chick predation on the periphery was also noted for guanay (*Phalacrocorax bougainvillei*, Phalacrocoracidae) (Andrewartha and Birch 1954). Through cooperation, larger colonies can also provide more effective defense for a given amount of individual energy expenditure. Allaine (1991) found that the percentage of time spent on colony defense by individual black-headed gulls (*Larus ridibundus*, Laridae) decreased with colony size, and the individual risk in small colonies was higher due to fewer birds participating in defense. Larger nesting colonies have also been found to provide protection against interspecific brood parasitism (laying eggs in the nest of another species). In a study of diederik cuckoo (*Chrysococcyx caprius*, Cuculidae) brood parasitism on red bishops (*Euplectes orix*, Ploceidae), Lawes and Kirkman (1996) found that rates of parasitism were negatively related to colony size. They contended that 'corporate vigilance and defense of large colonies probably prevents any significant parasitism from taking place in a population.'

Table 2 A summary of the evidence for impaired group dynamics at low densities.

Description	Source
Penguin, guanay (<i>Phalacrocorax bougainvillei</i>), black-headed Gull (<i>Larus ridibundus</i>), black brant (<i>Branta bernicla nigricans</i>), kittiwake (<i>Rissa tridactyla</i>), common guillemot (<i>Uria aalge</i>) Reduced edge and better defense increases reproductive success in larger breeding colonies	Emslie <i>et al.</i> (1995), Andrewartha and Birch (1954), Allaine (1991) Raveling (1989), Porter (1990) Birkhead (1977)
Red bishops (<i>Euplectes orix</i>) Less brood parasitism by cuckoos observed for larger colonies	Lawes and Kirkman (1996)
Sockeye salmon (<i>Oncorhynchus nerka</i>) Simulation model predicts longer school formation times for juveniles in lakes when density is low	Parkinson (1990)
Hatchery Atlantic salmon (<i>Salmo salar</i>) smolts Smolts released into larger shoals of natural smolts had higher survival	Hvidsten and Johnsen (1993)
Silvery minnows (<i>Hybognathus nuchalis</i>) Largemouth bass (<i>Micropterus salmoides</i>) took much longer to make a capture as school size increased	Landeau and Terborgh (1986)
Lake Malawi cichlids Joining schools allowed individuals access to better feeding sites	Marsh and Ribbink (1986)
Pronghorn antelope (<i>Antilocapra americana</i>) Groups that are too small tend to stampede instead of forming more effective defensive bands	Andrewartha and Birch (1954)
Dwarf mongooses (<i>Helogale parvula</i>) Higher juvenile survival in larger groups (potentially due to assistance from nonreproductive members)	Rood (1990)
Spider (<i>Anelosimus eximius</i>) Increased offspring survival for larger groups	Avilés and Tufiño (1998)
African wild dogs (<i>Lycan pictus</i>) Increased hunting efficiency with larger populations	Creel and Creel (1995)
Samango monkeys (<i>Cercopithecus mitis</i>) Higher instance of infanticide at lower densities	Swart <i>et al.</i> (1993)
Humans (Mennonite communities in the United States) Smaller Mennonite communities were less likely to persist due to increased contact and intermarriage with outsiders	Allee <i>et al.</i> (1949)

Schooling in fishes is another often-cited example of advantage in numbers. The mere fact that schooling is so prevalent suggests that it increases survival or reproductive success. If local densities are then reduced to the degree that school sizes are reduced, schooling becomes a depensatory mechanism. During the lake phase of their life history, juvenile sockeye salmon (*Oncorhynchus nerka*, Salmonidae) form schools during the day that break up at dusk. Parkinson (1990) constructed a model of school formation at dawn which predicted that lower population levels would result in longer school formation time and smaller schools, both resulting in higher mortality due to predation. Perhaps the most commonly described benefit of schooling is the reduced effectiveness of predators due to sensory confusion. In a laboratory study on predation of

largemouth bass (*Micropterus salmoides*, Centrarchidae) on silvery minnows (*Hybognathus nuchalis*, Cyprinidae), the bass took much longer to make a capture as the size of the minnow schools increased (Landeau and Terborgh 1986). Schooling can also provide access to higher quality food. Marsh and Ribbink (1986), in a study of Lake Malawi cichlids, observed that individuals were only able to gain access to aggressively defended, higher quality grazing sites when they joined a school.

There are many examples of beneficial terrestrial aggregations as well. Pronghorn antelope (*Antilocapra americana*, Antilocapridae), in groups of more than 12–15 animals, form a defensive band when attacked by wolves. In smaller groups they tend to stampede, providing easier targets for predators (Leopold 1933; p. 86). In the case of the dwarf mongoose (*Helogale*

parvula, Herpestidae) Rood (1990) found that juvenile survival was higher in larger groups. He noted that helpers assisted juveniles in finding food, acted as baby sitters (chasing off ground predators), and in some cases provided an additional supply of milk (lactating subordinate females). This increase in juvenile survival was offset by fact that only one pair in a pack reproduces leading to approximately constant per-capita young reared across the range of group sizes (it was lower for the largest groups). However, adult survival also increased with group size (probably due to better predator detection and mobbing) suggesting that the overall population growth rate may be higher when average pack size is larger. These results are supported by the more recent work of Clutton-Brock *et al.* (1999). They observed that in a year of low rainfall, all groups of meerkats (*Suricata suricatta*, Herpestidae) with less than nine individuals became extinct. Increased survival of young for larger group sizes was also found for the spider *Anelosimus eximius* (Theridiidae) (Avilés and Tufiño 1998). Offspring survival increased from about 4% for colonies of 10 or fewer to 18% to 24% for colonies between 51 and 107 individuals. A decreasing trend in the average number of egg sacks per female as a function of colony size eventually offset this advantage, producing highest individual fitness at intermediate colony sizes.

In a number of social hunters, hunting efficiency increases with population size. In a study of African wild dogs (*Lycan pictus*, Canidae), Creel and Creel (1995) found that 'hunting success, prey mass and the probability of multiple kills increased with number of adults. Chase distance decreased with number of adults.' This resulted in an increased efficiency with per-capita consumption per kilometer chased increasing as a function of pack size until peaking close to the modal adult pack size.

In order to make the link between reduced performance in smaller groups (herds, schools, packs or colonies) and depensation, it is necessary to use the results from groups of different sizes to imply what would happen to a single group if it experienced these different sizes (using spatial patterns to imply temporal patterns). This relies on the assumption that all differences between these groups are due to size.

Conditioning of the environment

Some organisms, when present in sufficient numbers, are able to modify their environment in a way that increases their survival or reproductive potential

(Table 3). When populations of these species are reduced to low densities, their ability to condition their environment is reduced, leading to depensation. A classic example of this mechanism occurs in many of the sap-feeding insects (phloem-feeding homoptera). By forming feeding aggregations on plants, they stimulate the flow of sap to their feeding sites, increasing the flow of sugars by as much as 80 times (Tonkyn 1986). This ability to feed more effectively at higher densities has been shown for a number of species (Andrewartha and Birch 1954; Wilbur 1977; Stamou and Asikidis 1989). When American bullfrog (*Bufo Americanus*, Bufonidae) larvae were raised at six different densities, Wilbur (1977) found that average body size decreased at low densities. He hypothesised that 'butting behaviour observed during feeding facilitates feeding because the substrate is stirred up, suspending food that larvae can filter from the water.' For populations of the oribatid mite, *Scheloribates latipes* (Scheloribatidae), Stamou and Asikidis (1989) hypothesised that, at higher densities, random contact between individuals caused increased mobility and therefore efficiency in searching for food. This was supported by experiments that showed a decrease in mite survival at low densities. Based on observed densities in the field they concluded that wild populations would probably be experiencing predominantly positive density feedback (i.e. depensation).

When temperatures are low enough to increase mortality, some animals form aggregations. By packing closely together they expose a lower percentage of surface area and are able to maintain a higher temperature within the aggregation than would be possible as individuals. In laboratory tests bobwhite quail (*Colinus virginianus*, Phasianidae) in large coveys (standing wing to wing in a circle with tails towards the centre) survived extremely low temperatures that kill individuals and smaller coveys (Allee *et al.* 1949).

Walters and Kitchell (2001) propose that the adults of some large fish populations may prey on forage species which compete with, or prey on, its juveniles. Decreasing the population may therefore reduce survival of the juveniles (due to more competition or predation) leading to depensation. They label this mechanism, cultivation depensation.

In a recent study of chum salmon (*Oncorhynchus keta*, Salmonidae) by Montgomery *et al.* (1996), a mechanism was proposed that linked increased spawner densities to higher embryo survival. They found that redd digging reduced grain mobility, thus

Table 3 A summary of the evidence for conditioning of the environment.

Description	Source
Phloem-feeding homoptera Feeding aggregations stimulate the flow of sap to their feeding sites, increasing the flow of sugars by as much as 80 times	Tonkyn (1986)
American Bullfrog (<i>Bufo Americanus</i>) At low densities body size increased with density	Wilbur (1977)
Grain borer (<i>Rhizopertha dominica</i>) High local densities are required to damage the grain surface sufficiently to begin feeding	Andrewartha and Birch (1954)
Oribatid mites (<i>Achipteria oudemansi</i>) and <i>Schelorbates latipes</i> Decreased fecundity and survival at low densities	Stamou and Asikidis (1989)
Bobwhite quail (<i>Colinus virginianus</i>) Individuals in larger coveys have a smaller proportion of their surface area exposed to the environment; this leads to higher survival in extremely cold conditions	Allee <i>et al.</i> (1949)
Salmon Spawning salmon carcasses provide marine derived nutrients that increases the productivity of the spawning streams. This may feed back to spawners in future generations through increased juvenile survival	Bilby <i>et al.</i> (1996), Larkin and Slaney (1997), Cederholm <i>et al.</i> (1999)
Chum salmon (<i>Oncorhynchus keta</i>) Redd digging reduces grain mobility decreasing the chances of stream-bed scour and therefore excavation of salmon embryos	Montgomery <i>et al.</i> (1996)

decreasing the chances of stream-bed scour and excavation of salmon embryos. They concluded that 'Such a feedback between salmon spawning and bed mobility would make it increasingly difficult to reverse declining populations because decreased spawning activity would increase susceptibility to scour, leading to higher embryo mortality.'

Another way that salmon condition their environment is through marine nutrients brought to the fresh water rearing grounds by returning adults (Larkin and Slaney 1997; Cederholm *et al.* 1999). For example, in a Western Washington stream, Bilby *et al.* (1996) found that 31% of Nitrogen and 40% of Carbon in juvenile coho was of marine origin and the growth rate of the juvenile coho doubled after the adults spawned. This nutrient feedback within salmon populations may lead to depensation (Mathisen 1972; Larkin and Slaney 1997; Cederholm *et al.* 1999).

Predator saturation

Handling time, gut capacity and digestive constraints limit the amount of prey that a predator population can consume in a given interval of time. If the prey density exceeds this limit, then the predator population is said to be saturated (or swamped or satiated) and further increases in prey density will lead to reductions in the proportion of

prey lost to predation. The mortality caused by this type of predation is therefore depensatory (depensatory predation). Increases in the predator population in response to increasing prey density (a numerical response) will tend to counteract this. However, there are situations in which this response either is delayed or does not occur at all. For example, if the prey population is only available to the predator for a small period of time during the year, the predator may be limited by other more consistent resources. Migrating Pacific salmon smolts, for example, are only available to many freshwater predators during a brief period each year on their way to the ocean. The predator populations, limited by less abundant year-round prey sources, are therefore unable to grow in response to increases in the size of the salmon population.

There are a number of studies that support predator saturation as a depensatory mechanism (Table 4). Wood (1987) examined predation by the common merganser (*Mergus merganser*, Anatidae) on juvenile Pacific salmon during seaward migration in two streams where populations were enhanced by hatcheries and spawning channels. He found that maximum rates of salmon mortality, due to merganser predation, declined with increased salmon abundance (i.e. depensatory mortality). In a similar study of predation on juvenile chum salmon, Fresh

Table 4 A summary of the evidence for predator saturation.

Description	Source
Juvenile Pacific salmon Maximum rates of salmon mortality, due to merganser predation, declined with increased salmon abundance	Wood (1987)
Chum salmon (<i>Onchorhynchus keta</i>) Found evidence of predator saturation and concluded that survival could be increased in smaller streams and rivers through enhancement projects	Fresh and Schroder (1987)
Sockeye salmon smolts (<i>Onchorhynchus nerka</i>) Percentage mortality due to arctic char (<i>Salvelinus alpinus</i>) in a small Alaskan stream decreased above a certain density of prey	Ruggerone and Rogers (1984)
Salmon Several Native American subsistence fisheries in British Columbia behave like predators that become saturated	Peterman (1980)
Fish By forming larger schools the probability of detection is decreased leading to lower mortality due to predation	Brock and Riffenburgh (1963)
Spruce budworm (<i>Choristoneura fumiferana</i>) The observed cyclic behaviour of the population was approximately reproduced using a model with predator saturation	May (1977) Ludwig <i>et al.</i> (1978)
Pelagic fish. A simple population model with depensatory predation and red noise mimicked the roughly 50 years cycles observed in some pelagic fish populations	Steele and Henderson (1984)

and Schroder (1987) released different-sized groups of juvenile chum salmon into a natural and artificial stream. They found evidence of predator saturation, and concluded that survival could be increased in smaller streams and rivers through enhancement projects. An example of depensatory predation in a natural stream without enhancement was provided by Ruggerone and Rogers (1984). Percent mortality due to arctic char (*Salvelinus alpinus*, Salmonidae) in a small Alaskan stream decreased above a certain density of prey (sockeye salmon smolts).

Schooling provides another possible method of swamping a predator population (Brock and Riffenburgh 1963). When the size of a school decreases, a predator or group of predators that encounters that school will be able to consume a larger proportion of the school before they are satiated, therefore inflicting a higher per-capita mortality.

Although not direct evidence of depensation, the cyclic behaviour of Fraser River (British Columbia) sockeye populations has been attributed to age-class interactions and depensatory predation (for a review see Ricker 1997). Applying a statistical model to sockeye salmon data from one Fraser river lake (Chilko lake), Crittenden (1994) found that incorporating depensatory mortality along with weak compensation during smolt migration ex-

plained a significant amount of the variation in adult returns. Mortalities due to human fisheries may also be depensatory. Peterman (1980) showed that several Native American subsistence fisheries in British Columbia behave like predators that become saturated. He used this result to explain the depensatory dynamics of the fished stocks suggested by data.

Depensatory predation is often implicated in situations where a population appears to alternately exist at two stable equilibria. The spruce budworm (*Choristoneura fumiferana*, Tortricidae), for example, is a forest defoliator that irrupts approximately every 40 years. This cycle, between two population extremes, is an often-cited example of depensatory dynamics produced by a saturated predator (May 1977). Using a model of spruce budworm dynamics that included a saturated predator, and accounting for forest growth, Ludwig *et al.* (1978) were able to approximate the observed cycles. Similar cyclic shifts between two densities has been observed for a number of pelagic fish populations (Steele and Henderson 1984). Using a simple population model with depensatory predation and red noise (common in environmental variation) Steele and Henderson (1984) were able to reproduce the roughly 50-year cycles observed in these populations.

The studies described above, where simple population models are used to mimic observed patterns in abundance, provide very little support for depensatory predation and should be viewed more as hypotheses for further investigation than evidence.

Difficulty detecting depensatory population dynamics

Except for populations of invertebrates grown in the laboratory (e.g. Odum and Allee 1954), there is little convincing evidence of populations that exhibit depensation. In a few recent studies, demographic data from many different populations were used to determine the prevalence of depensation within different groups of populations (Fowler and Baker 1991; Myers *et al.* 1995; Sæther *et al.* 1996). Fowler and Baker (1991) compiled fecundity and mortality data for large mammal populations which had experienced population levels $\leq 10\%$ of the historically observed maxima. For the 12 populations they found that met this criterion, there was no evidence of depensation. A similar process was repeated by Sæther *et al.* (1996) for birds. Instead of 10% of the historical maximum, they used 15%, and they required a linearly decreasing trend in fecundity, clutch size or recruitment rate. Again, they found no evidence of depensation. In what is by far the largest study of this type, Myers *et al.* (1995) used stock–recruit data collected from 128 commercially exploited marine and anadromous fish populations to assess the prevalence of depensation. Using a likelihood-ratio test, they rejected in favour of depensation for only three of the populations.

These three studies seem to suggest that depensation is rare. There are, however, a number of reasons why depensation may be difficult to detect using these types of demographic data. Environmental and demographic stochasticity make it difficult to detect the underlying population dynamics over time. This is especially true of depensation which occurs at most over only a small portion of the range of densities. In addition, the 10% and 15% levels set by Fowler and Baker (1991) and Sæther *et al.* (1996) may be above the densities at which many of these populations exhibit depensation. For these reasons, the statistical power of tests for depensation will tend to be low, potentially missing many instances of depensation. Myers *et al.* (1995) found that the probability of detecting moderate depensation if it did occur was > 0.95 for only 26 of the 128 stocks they

examined (and this may be an overestimate, see Shelton and Healey 1999). Liermann and Hilborn (1997) used a meta-analysis to describe the uncertainty in depensation for the populations used by Myers *et al.* They grouped the populations into four taxa and calculated a distribution describing the uncertainty in depensation for a generic population from each taxon. For all four taxa they found that there was neither strong evidence supporting nor rejecting the existence of depensation.

Because the populations used in these studies are not necessarily representative of all populations of large mammals, birds, and fishes, caution should be used when generalising the results. For example, the populations used in the Myers *et al.* (1995) and Liermann and Hilborn (1997) studies were all commercially fished populations. Populations which are not profitable to fish (e.g. too small, reproductive rate is too low, difficult to catch, or unpalatable) are therefore not represented. Generalising to all fish species would therefore be unjustified.

The scale at which populations are defined may also mask depensation. Frank and Brickman (2000) showed that the aggregate recruitment of several subpopulations may appear compensatory even if each of the subpopulations has depensatory recruitment.

Modelling depensatory mechanisms

In this section, we present mechanistic models for two of the depensatory mechanisms described above: reduced fertilisation success (Table 5) and predator saturation (Table 6). These are by far the most common types of depensation modelled in the literature. We will limit the scope of this review to models that are derived based on a mechanism, yet are relatively simple. Since it is very difficult to detect depensation, characterising it with complex (many-parameter) models will tend to be unreasonable for applied population dynamics problems. In particular, statistical analysis of population data will only be tractable with simpler models. Although the assumptions on which these simpler models are based will almost certainly be broken when modelling complex natural systems, by presenting a family of models for each mechanism it is more likely that one of these models will prove sufficiently flexible to approximate the variety of possible dynamics for a given population. If none of the models provides a satisfactory fit to the observed or hypothesised depensatory dynamics, their mechan-

Table 5 A summary of the different models of mate-finding success as a function of density.

Function	Source	Assumptions
$1 - e^{-aN}$	Dennis (1989) McCarthy (1997)	Density of mates does not change over time. All individuals have identical probabilities of finding a mate.
$\frac{N}{1 + aN}$	Dennis (1989) McCarthy (1997) Lewis and Kareiva (1993)	Density of mates does not change over time. Searching time or searching efficiency is different between individuals. It follows an exponential distribution. All individuals have identical probabilities of finding a mate Potential mates are depleted over time due to pairing. Proportion of females in the population is 0.5.
$\frac{(1-r)(e^{aN(1-2r)} - 1)}{(1-r)e^{aN(1-2r)} - r}$	McCarthy (1997)	All individuals have identical probabilities of finding a mate Potential mates are depleted over time due to pairing. Proportion of females in the population is r .

Table 6 A summary of the different functional response models.

Type	Function	Source	Assumptions
I	$E = \begin{cases} aTN & \text{if } N < \frac{1}{ab} \\ T/b & \text{if } N \geq \frac{1}{ab} \end{cases}$	Holling (1965)	Rate of discovery is proportional to N Limited by digestion
II	$\frac{aTN}{1 + abN}$ $b(1 - e^{-aN})$ $E = \frac{-\ln[(1 - e^{-aN})e^{-aKPT} + e^{-aN}]}{a}$	Holling (1959b) Gause (1934, see Holling 1959a), see Holling (1959a, b) and Ivlev (1961) Royama (1971)	Rate of discovery is proportional to N Limited by handling time Rate of consumption is proportional to $K - N$, where K is the maximum rate of consumption. The Gause/Ivlev type II functional response modified to account for depletion.
III	$E = \frac{kN^d}{x + N^d}$ $E = \frac{cTN^2}{1 + dN + cbN^2}$ $E = \frac{TN}{e^{-gN} + bN}$	Real (1977) Hassell <i>et al.</i> (1978) Fujii <i>et al.</i> (1978)	A learning predator is analogous to an enzyme reaction where the rate at which the enzyme acts is related to the number of substrate particles that it has already bonded to. Holling's type II model with rate of discovery (a) equal to $cN/(1 + dN)$ Holling's type II model with rate of discovery (a) equal to E^{gN}

istic derivations provide a logical framework for adding incremental complexity.

Reduced fertilisation success

Several models describing reduced probability of success at low densities have been proposed (Table 5). Although their derivations differ, they can all be viewed as generalisations of a basic random-encounter model.

If an individual systematically searches an area a for mates, and the potential mates are randomly distributed in space, the probability of encountering x mates in area a is described by the Poisson distribution:

$$(1) \quad P(x) = \frac{\lambda^x e^{-\lambda}}{x!} = \frac{(baN)^x e^{-baN}}{x!}.$$

The rate of encounters (λ) is proportional to density (N) and the area searched (a) (i.e. $\lambda = baN$, where b is a constant of proportionality). For many species, a single encounter is sufficient to achieve full reproductive potential. In this case, the probability of at least one encounter is of interest:

$$(2) \quad \begin{aligned} P(x > 0) &= 1 - P(x = 0) \\ &= 1 - \frac{(baN)^0 e^{-baN}}{0!} \\ &= 1 - e^{-baN}. \end{aligned}$$

This simple negative exponential function rises from the origin to an asymptote. An increase in the density or area searched elevates the rate of encounter, causing the curve to rise more rapidly (Fig. 3a). Because this relationship is only dependent on $P(x = 0)$, the model is still valid when the probability of an encounter is dependent on the number of previous encounters (Dennis 1989). This expands its applicability to situations in which potential mates are either more clumped (the probability of encounter increases with the number of previous encounters) or more regularly distributed (the encounter rate decreases with encounters).

Accounting for individual differences in the encounter rate

The relationship between density and encounter rate will vary among individuals in a population. For example, in the case of wind-dispersed pollen, if the probability of a pollen grain settling is equal for each small increment that it moves away from the parent plant, then the distances dispersed (similar to the area searched, a) by different pollen grains follows an exponential distribution (McCarthy

1997). This can be accounted for by using a mixed probability distribution (Dennis 1989; McCarthy 1997). The probability of encounter is averaged over the distribution of dispersal distances [$f(a)$]:

$$(3) \quad P(x > 0) = \int_0^{\infty} (1 - e^{-baN})f(a) da$$

$$= \int_0^{\infty} (1 - e^{-baN}) \frac{1}{\lambda} e^{-\frac{a}{\lambda}} da$$

$$= \frac{N}{\frac{1}{b\lambda} + N}$$

Here, λ is the mean and standard deviation of the exponential distribution describing the dispersal distance or 'area searched'. By replacing distance dispersed with area searched (representing individual differences in searching efficiency), this could be applied to species in which individuals actively search. Dennis (1989) presented the gamma and Raleigh functions as two additional distributions

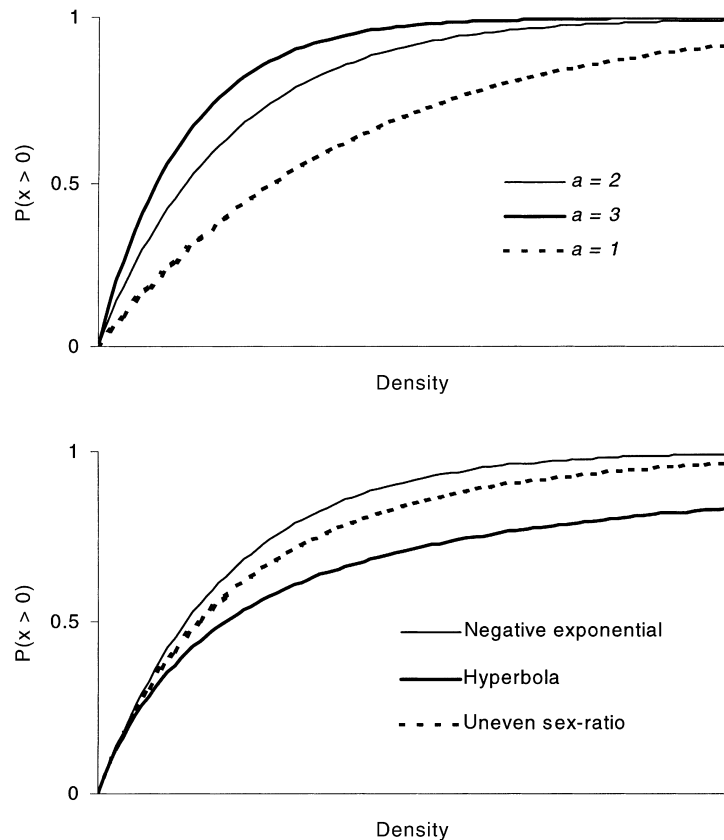


Figure 3 The probability of a female finding a mate (as a function of density) is calculated under a number of different assumptions. (Upper curves) The negative-exponential model with three different values of a (area searched in arbitrary units). (Lower curves) Models representing three different sex ratios: (i) negative exponential, when there are unlimited males ($r \rightarrow 0$); (ii) a hyperbola when the female-to-male ratio is 1 : 1 ($r = 0.5$), and (iii) the general model when the female-to-male ratio is 3 : 7 ($r = 0.3$).

that could be used to represent individual differences in dispersal distance or searching efficiency.

Depletion of potential mates

In a monogamous mating system, where pairs are formed, the number of available mates decreases with area searched (or time). Veit and Lewis (1996) account for the decreasing pool of mates by modelling the mate-finding process as a reaction. Using the law of mass action, the rate at which pairs (M) are formed is proportional to the densities of the remaining males and females (reactants). Given a population of N , and a sex ratio of 1 : 1 this leads to the differential equation:

$$(4) \quad \frac{dM}{dt} = k \left(\frac{N}{2} - M \right)^2.$$

With initial condition $M(0) = 0$, the proportion of individuals that have found mates by time T (or the probability of finding a mate by time T) is:

$$(5) \quad P(x > 0) = \frac{N}{\frac{2}{Tk} + N} = \frac{N}{\frac{1}{a} + N}.$$

In a more biologically motivated but mathematically similar derivation, McCarthy (1997) allows for an unequal sex ratio. Defining r as the proportion of the population that is female, and using the notation above, this leads to the more general differential equation:

$$(6) \quad \frac{dM}{dt} = k[rN - M][(1 - r)N - M].$$

The probability of a female finding a mate is now:

$$(7) \quad P(x > 0) = \frac{(1 - r)(e^{NkT(1-2r)} - 1)}{(1 - r)e^{NkT(1-2r)} - r}$$

$$= \frac{(1 - r)(e^{aN(1-2r)} - 1)}{(1 - r)e^{aN(1-2r)} - r}.$$

For a 1 : 1 sex ratio this reverts to the hyperbola above (equation 5). As expected, when there are more males than females ($r < 1$), the probability of a female finding a mate increases (Fig. 3b). If there are many more males than females (r approaches 0), then depletion of the pool of potential mates is no

longer significant, and the equation simplifies to the negative exponential (Fig. 3b).

Multiple matings

For some species, more than one mating is necessary to achieve full reproductive potential. Park (1933), for example, found that female tribolium (*Tribolium confusum*, Tenebrionidae) produce 10 times more eggs after two matings when compared to a single mating. In order to calculate the expected reproductive success for this type of organism, a function, $f(x)$, describing the proportion of the reproductive potential achieved with $x = 0, 1, 2, 3 \dots$ encounters is necessary. Multiplying this by the probability of x encounters and summing over encounters produces the expected reproductive success:

$$(8) \quad E(\text{reproductive success}) = \sum_{x=0}^{\infty} [P(x)f(x)].$$

Predator saturation

The main elements unique to modelling predation are the two functions describing (i) the response of the predator to the prey density (the numerical response) and (ii) the rate at which prey are consumed as a function of prey density (the functional response). As discussed in the evidence section, depensation caused by predation occurs when the predator is swamped. This can happen when growth of the predator population, in response to increased prey density, is either delayed (perhaps due to a much slower growth rate), or is constrained to a maximum level by some other limiting factor besides the availability of the prey of interest. I will focus on the functional response in this section, assuming the predator population is constant (Table 6).

There is a maximum rate at which any predator can consume prey. So all functional response curves should rise from zero towards a maximum. Holling (1965) described three such curves (Fig. 4).

Type I functional response curves

The type I functional response has been attributed to filter feeders, where filtering (or searching) can continue while prey is being processed (handled). Assuming that the rate of encounter is proportional to the density of prey, and that each prey encountered is consumed, the rate of consumption will increase linearly with prey density until the

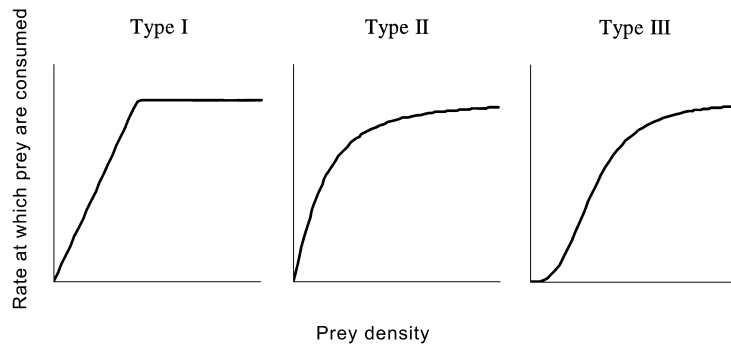


Figure 4 Holling's three functional responses (Holling 1965).

prey is captured at a rate faster than it can be processed. For all densities above that point, consumption is limited only by the rate of processing. Using Holling's notation this becomes

$$(9) \quad E = \begin{cases} aTN & \text{if } N < \frac{1}{ab} \\ T/b & \text{if } N \geq \frac{1}{ab} \end{cases}.$$

Here, b is the processing rate, T is the total time available, N is the prey density, and a is the search rate.

Type II functional response curves

For animals that must handle each prey before continuing to search (most animals), the proportion of the total time devoted to prey handling gradually increases with density. This rounds off the sharp corner of the type I response, producing the type II functional response (Fig. 4). Holling (1959b) used two simple assumptions to construct a model that accounted for handling time. These assumptions were: (i) the number of prey eaten (E) is proportional to the time available for searching (T_s) and the density of prey (N), and (ii) the time available for searching (T_s) is equal to the total time available (T_t) minus the time spent handling prey (bE , b is time spent handling an individual prey). Combining these assumptions leads to the equation:

$$(10) \quad E = a(T_t - bE)N.$$

Solving for E and simplifying produces the familiar asymptotic curve:

$$(11) \quad E = \frac{aT_t N}{1 + abN}.$$

This is commonly referred to as Holling's disk equation due to the sandpaper disks Holling used in an experiment designed to verify the model. The parameter a multiplied by the prey density, N , gives the rate of discovery of prey by predators.

Both Gause (1934; see Holling 1959a) and Ivlev (1961) hypothesised that hunger regulated the rate of consumption. For a given number of predators, they suggested that there is a maximum possible number of prey consumed (K), and that the rate of consumption with respect to prey density is proportional to that maximum (K) minus the number already consumed (prey eaten = E). This translates into the differential equation:

$$(12) \quad \frac{dE}{dN} = a(K - E).$$

With the initial condition $E(0) = 0$, the solution to this differential equation is the negative exponential function,

$$(13) \quad E = K(1 - e^{-aN}).$$

Sjöberg (1980) demonstrated that the type I functional response and the Holling and Gause type II functional responses can all be viewed as special cases of a queue model.

Type III functional response curves

For many predators, the functional response curve is concave upwards at low densities, producing an overall sigmoid or type III shape (Fig. 4). A couple of explanations have been proposed. Predators sometimes consume a disproportionate amount of a more abundant prey, largely ignoring the less common prey. This phenomena, coined 'switching' by Murdoch (1969), reduces predation at low prey densities, leading to a type III functional

response. Two potential causes for switching are, more efficient searching for the higher density prey due to learning (Holling 1959a; Tinbergen 1960), and differing locations of the abundant and less abundant prey (Royama 1970).

Reduced intraspecific competition at low densities can also lead to a type III functional response. Less activity (e.g. looking for food) afforded by less competition for resources, reduces the risk of predation and therefore lowers the rate of mortality.

The type III response was initially attributed mainly to vertebrate predators (e.g. Holling 1965). However, there is evidence that this shape is also common in invertebrates (Hassell *et al.* 1977).

Real (1977) draws on the similarity between predation and enzyme kinetics to construct a type III functional response curve. He considers the substrate as the prey, the enzyme as the predator, and the product as the consumption of a prey. If the enzyme has multiple sites, and the binding of one substrate molecule facilitates the binding of another on the same enzyme, then it is called an allosteric enzyme (haemoglobin is an example). He compares this to predator learning (described above), where the more of a particular prey a predator catches, the more efficient it becomes at catching that prey. Under some simple assumptions the rate at which the product is produced (or prey is eaten) is described by the Hill equation:

$$(14) \quad E = \frac{kN^d}{x + N^d}.$$

This can be rewritten as a generalisation of the disk equation:

$$(15) \quad E = \frac{(aN^{d-1})TN}{1 + (aN^{d-1})bN},$$

where the instantaneous rate of discovery is an increasing function of prey density, aN^{d-1} , instead of a constant, a , as in the standard disk equation (Real 1977).

Hassell (1978) arrives at a similar model by assuming that the lower 'reward rate' experienced at the lowest prey densities reduces the search rate (based on observations of insect predation). This assumption means replacing the

instantaneous rate of discovery (a) in the disk equation of Holling with an increasing function of prey density:

$$(16) \quad a = \frac{cN}{1 + dN}.$$

This produces the type III functional response:

$$(17) \quad E = \frac{cTN^2}{1 + dN + cbN^2}.$$

This general approach could be used to create a family of curves where a and b (the instantaneous rate of discovery and handling time) are replaced by increasing and decreasing functions of prey density, respectively.

Incorporating the number of predators into the functional response curve

If there is no predator interaction, the number of predators can be included in these functional response curves by simply multiplying the functional response by the number of predators. When the predators interfere with each other this simple form breaks down and requires additional model complexity (see for example Watt 1959).

Accounting for prey depletion over time

None of the functional response curves that have been presented to this point account for depletion of prey over time. As such, they can be viewed as describing the rate of consumption. For a population model described by a differential equation, this would be the appropriate form. When used in discrete time models, where depletion becomes an issue, these curves may be sufficient if the change in prey density during the time interval of interest is small (i.e. depletion is minimal). This could occur, for example, when the number of prey is very large relative to consumption, the time interval is small, or the predator systematically searches its environment avoiding previously depleted areas.

In situations where predation does cause a significant decline in prey density (over the period of interest), this depletion should be accounted for in the models. This can be done by modelling prey depletion as a differential equation using one of the instantaneous functional response functions from

above (Royama 1971). For example, using the Gause/Ivlev type II functional response, with predators P and maximum percapita rate of consumption K , produces the differential equation:

$$(18) \quad \frac{dN}{dt} = -PK(1 - e^{-aN}).$$

Integrating from time 0 to T with initial and terminal conditions, $N(0) = N$ and $N(T) = N - E$, and solving for E results in the number of prey consumed in time T (accounting for depletion):

$$(19) \quad E = \frac{-\ln[(1 - e^{-aN})e^{-aKPT} + e^{-aN}]}{a}.$$

For small time intervals (small T) there is no appreciable difference between the shape of this model (equation 19) and the instantaneous functional response (equation 18). As T increases, however, the number of prey consumed approaches

the total number of prey available (N) (Fig. 5). This produces a curve with a much more linear ascending limb (Fig. 5).

Unfortunately, using the same approach for other functional responses presented above results in differential equations that are unsolvable (e.g. most of the type III functional response curves presented above), or solutions for which it is not possible to solve for E (e.g. Holling's disk equation). This limits their usefulness as components of population dynamics models.

This review of functional response curves is only a cursory look at this field. For a more structured and in-depth presentation see Royama (1971) and Hassell (1978).

The simple reduced fertilisation-success and predator-saturation models presented in this section were primarily developed to explain results of controlled experiments using arthropods or rodents. More detailed models (e.g. Holling 1965), though well suited for studying the processes, are generally not useful as components of population

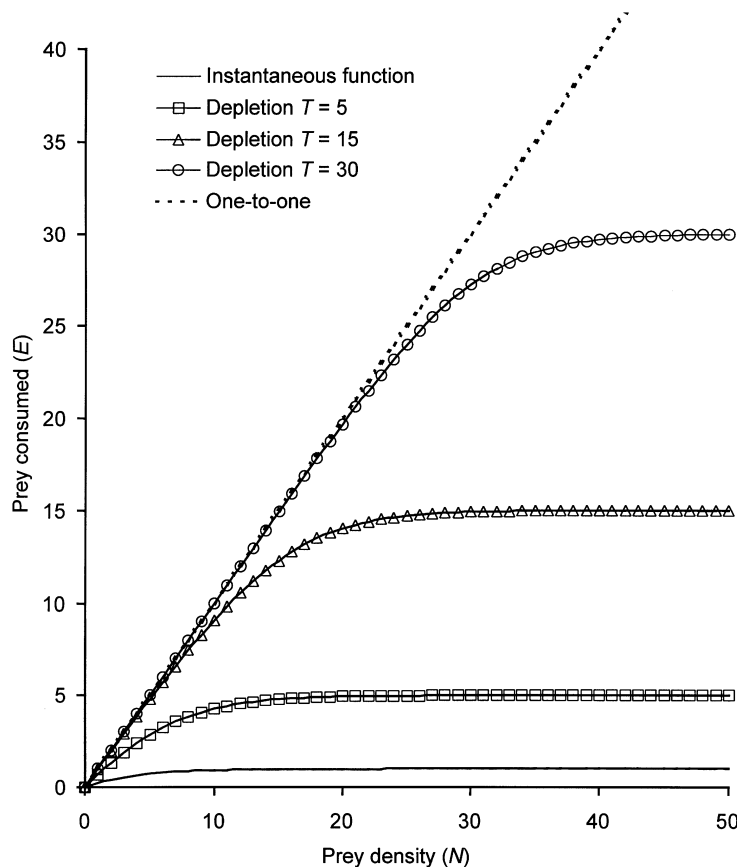


Figure 5 As the time interval (T) during which depletion occurs increases, the number of prey consumed approaches total number of prey available (N) (represented by the 1-to-1 line). This results in a more linear ascending limb.

dynamics models because of the significant increase in parameters that need to be estimated. Where the simple models above have been used to describe much more complex natural systems (e.g. Peterman and Gatto 1978; Norris and Johnstone 1998) the parameters lose their original meanings (e.g. rate of discovery, handling time and attack rate). However, the two- and three-parameter models presented above provide a broad range of shapes that should approximate many of the functional responses found in natural populations. Because the dynamics of different natural systems will vary considerably, model choice will be dependent on the specific population to be modelled. In situations where none of the models are appropriate, their mechanistic derivations provide a basis for generalisation.

Population models that include depensation

By embedding the models of depensation presented above into full population dynamics models (with reproduction and regulation), it is possible to investigate the effects of depensation on extinction probability (Jacobs 1984; Lande 1987; Dennis 1989; Lande *et al.* 1994), colonisation success (Jacobs 1984), spread of an invading species (Lewis and Kareiva 1993; Veit and Lewis 1996), pest control (May 1977), management of populations (May 1977; Botsford *et al.* 1993; Lande *et al.* 1994), and other questions that require modelling a population over time. These population dynamics models take the form of differential equations (May 1977; Jacobs 1984; Steele and Henderson 1984; Collie and Spencer 1993; Lewis and Kareiva 1993; Spencer and Collie 1997), and difference equations (Larkin *et al.* 1964; Parrish and MacCall 1978). They can include demographic and environmental variability (Larkin 1971; Steele and Henderson 1984; Dennis 1989; Lande *et al.* 1994), spatial structure (Lewis and Kareiva 1993; Veit and Lewis 1996), meta-population dynamics (Nickelson and Lawson 1998), age structure (Stamou and Asikidis 1989), and multi-species interactions (May 1977).

There are a number of different ways in which depensation can be introduced into a population dynamics model. I will illustrate four methods using two difference equation models commonly applied in the fisheries literature: the Beverton–Holt

(Beverton and Holt 1957) and Ricker (Ricker 1954) spawner–recruit (SR) functions. The methods are: (i) incorporating depensatory mechanisms into the differential equations from which the SR functions are derived; (ii) turning one or more of the SR model parameters into functions; (iii) creating a multistage model which includes a depensatory stage and (iv) assuming that both depensatory and compensatory effects are dependent on the same life-stage.

The Ricker and Beverton–Holt spawner–recruit models

Both the Ricker and Beverton–Holt spawner–recruit curves (Fig. 6) can be derived by starting with a differential equation describing survival from eggs (spawners times average fecundity, Sf) to recruits (the number of individuals, N , that survive to time T , $R = N(T)$).

$$(20) \quad \frac{1}{N} \frac{dN}{dt} = -a - bN \quad \text{Beverton-Holt}$$

$$(21) \quad \frac{1}{N} \frac{dN}{dt} = -a - bS \quad \text{Ricker}$$

The Beverton–Holt relationship assumes the per-capita rate of mortality is a linear function of the number of surviving fish (N) in the cohort (equation 20), while the Ricker model assumes per-capita survival is a linear function of the number of spawners (S) (equation 21). Integrating to the time of recruitment, T , and imposing the conditions $N(0) = Sf$ and $N(T) = R$ ($f =$ fecundity) produces the two familiar spawner–recruit relationships. The Beverton–Holt equation rises to an asymptote (Fig. 6):

$$(22) \quad R = \frac{S}{\frac{1}{p} + \frac{S}{c}}$$

Here it is parameterised in terms of the initial slope or productivity (p), and the asymptote or capacity (c). The Ricker curve rises to a maximum (g) before declining towards the ‘spawner’-axis (Fig. 6):

$$(23) \quad R = pS \exp\left(-\frac{S}{g}\right).$$

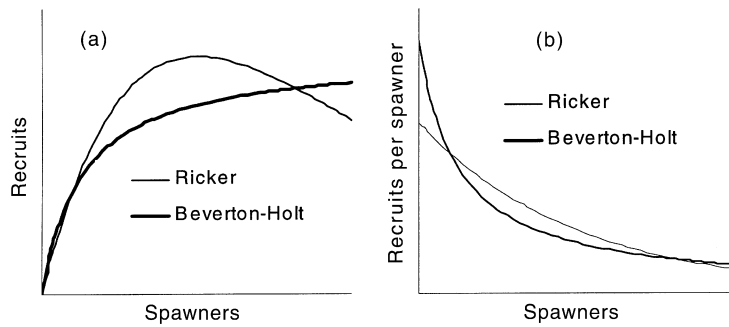


Figure 6 The Beverton–Holt and Ricker spawner–recruitment functions plotted as (a) recruits vs. spawners, and (b) recruits per spawner vs. spawners.

As in the Beverton–Holt equation, the parameter p is the initial slope.

For an spawner–recruits function to be depensatory, the per-capita rate of growth, or recruits per spawner, must be an increasing function over part of its domain. Expressed in terms of recruits per spawner the Beverton–Holt and Ricker models are both strictly decreasing functions therefore excluding the possibility of depensation (Fig. 6b).

Modifying the differential equation

One approach to adding depensation to these spawner–recruit functions is to modify the differential equations on which the Ricker and Beverton–Holt curves are based. This could be done by adding either a function of the current population size (N) or a function of spawners (S). Any function of N more complicated than a linear relationship will probably lead to a differential equation that cannot be analytically reduced to a SR function. This limits the usefulness of this technique when the depensatory mechanism acts during the juvenile stage. Because the number of spawners, S , is a constant in the differential equations above, adding a function of S does not make solving the differential equations any more difficult. There are many potential depensatory mechanisms that would be dependent only on the number of spawners (S). For example, when adding predation, this may be approximately true in populations where the adult and juvenile stages coexist and the number of juveniles is small compared to the adult population size. Adding predation to the Ricker model using Real’s (1977) type III functional response (May 1977; Emlen 1984) produces:

$$(24) \quad \frac{1}{N} \frac{dN}{dt} = -a - bS - \frac{mS}{h^2 + S^2}.$$

This reduces to the spawner–recruit function (Fig. 7):

$$(25) \quad R = pS \exp\left(\frac{S}{g} - \frac{mS}{h^2 + S^2}\right).$$

Here, m is the maximum level of predation, h is the number of spawners at which the predation is half of the maximum (m), and g is the maximum of the spawner–recruit curve in the absence of predation.

Turning parameters into functions

A second approach to incorporating depensation into these SR models is to allow the parameters of the models to be dependent on the number of spawners. One of the more commonly used depensatory models in the fisheries literature (Hilborn and Walters 1992; Thompson 1993; Myers *et al.* 1995; Liermann and Hilborn 1997) can be derived by replacing the productivity parameter (p) in the Beverton–Holt model (equation 22) with a geometrically increasing function of Spawners ($P = aS^{d-1}$) (Fig. 7b),

$$(26) \quad R = \frac{S}{\frac{1}{aS^{d-1}} + \frac{S}{c}} = \frac{S^d}{\frac{1}{a} + \frac{S^d}{c}}.$$

One objection to this model might be that productivity should not continue to increase unbounded but eventually level off to an asymptote. One flexible yet simple function that meets this criterion is Real’s type III functional response curve (equation 14). This leads to the SR model:

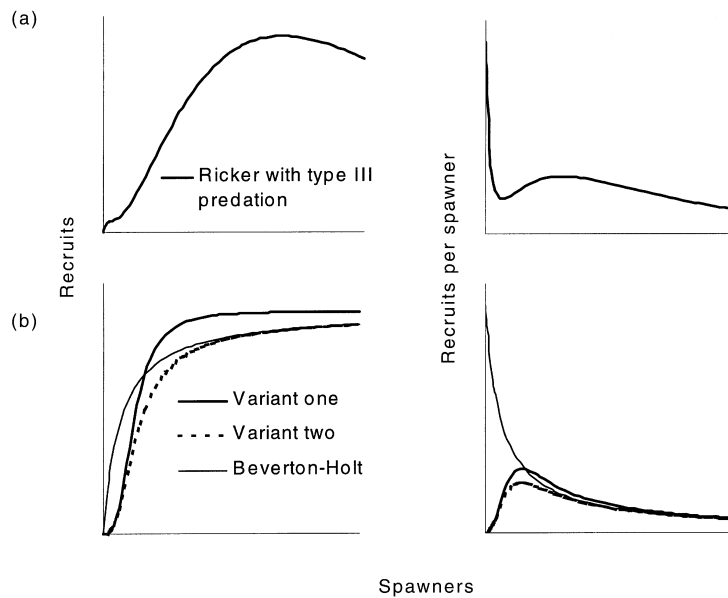


Figure 7 (a) Type III predation added to the Ricker model by modifying the differential equation (equation 21). (b) The Beverton–Holt model and two variants constructed by modelling p (productivity) as an increasing function of spawners.

$$(27) \quad R = \frac{S}{\frac{1}{\left(\frac{aS^{d-1}}{b^{d-1} + S^{d-1}}\right)} + \frac{S}{c}} = \frac{S^d}{\frac{b^{d-1} + S^{d-1}}{a} + \frac{S^d}{c}}$$

This curve is similar to the previous curve at low densities, but as S continues to increase it converges to the original nondepensatory model, rising less steeply than the previous curve (Fig. 7b). The parameter a is the maximum productivity, and b is the spawner level at which the productivity is half of a .

Modelling multiple life history stages

The third method of incorporating depensation involves breaking the recruitment process into multiple sub models, representing different stages of the life history. Larkin *et al.* (1964) demonstrated the variety of hypothetical spawner–recruitment relationships that can be constructed from simple two and three stage models that include a depensatory stage (Fig. 8a).

Peterman (1977) and Grout (1993) use two stages to include predation in a salmon life history model. The standard Ricker equation is used to model the population up to the point of predation (N). Predation is then included in a second stage using Real’s (1977) type III functional response.

$$(28) \quad N = S \exp \left[r \left(1 - \frac{S}{k} \right) \right]$$

$$(29) \quad R = N - \frac{aN^2}{b^2 + N^2}$$

Peterman (1977) showed that for a plausible parameterisation this system can produce two stable equilibria (Fig. 8b).

The depensatory mechanism may also occur as a first stage. For example, if a salmon population experiences reduced mate finding success it would occur before juvenile competition (a potential source of compensation). This can be modelled using a hyperbola (equation 3) to describe mate-finding success (Dennis 1989; McCarthy 1997) and the Beverton–Holt model (equation 22) (another hyperbola) to describe the compensatory second stage:

$$(30) \quad N = \frac{S}{h + S} S$$

$$(31) \quad R = \frac{N}{\frac{1}{p} + \frac{N}{c}}$$

Here N is the number of spawners that find mates, and the parameter h is the density at which

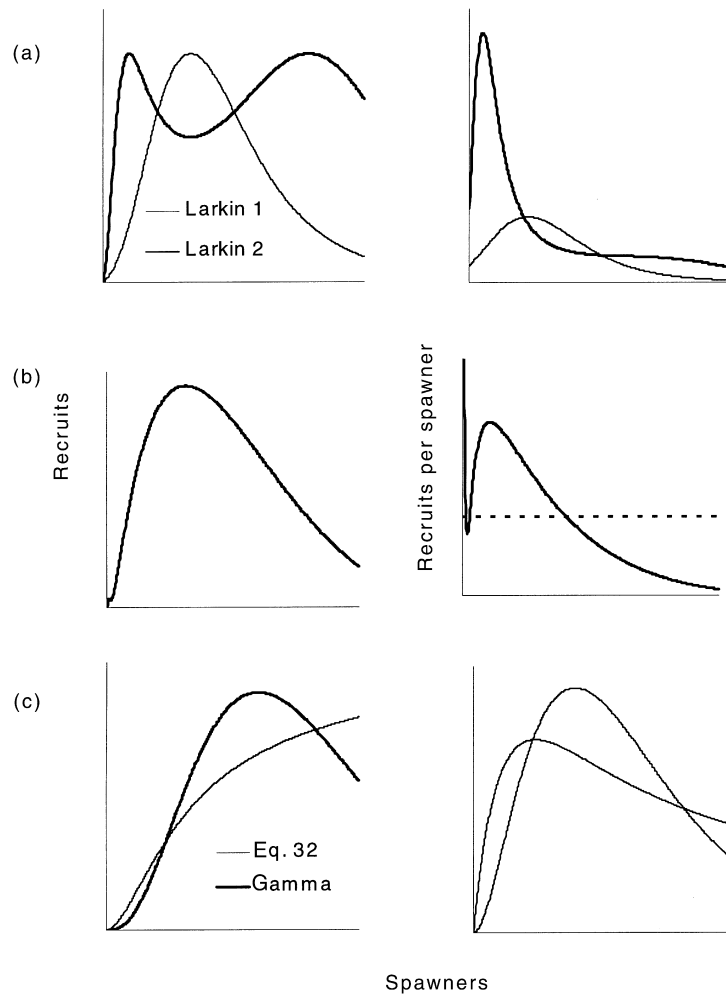


Figure 8 (a) Three different parameterisations of Larkin's two-stage model; (b) Peterman's model incorporating predation (equation 28) and (equation 29) with the replacement line (dotted); (c) a model described in this paper (equation 33) and Saila's model (equation 34).

half of the spawners find mates. Combining these two stages produces:

$$(32) \quad R = \frac{S^2}{\frac{h+S}{p} + \frac{S^2}{c}}$$

In some cases, three or more stages might be appropriate. A depensatory predation stage, for example, may occur between two compensatory life history stages.

Depensatory and compensatory effects dependent on the same life history stage

When more than one density regulating mechanism is dependent on the same life history stage, the functions can be multiplied together (e.g. Prout

and McChesney 1985; Bjorkstedt 2000). For example, mate-finding success and competition for spawning habitat might both be viewed as functions of the number of potential spawners arriving at a stream. Using the negative exponential function (equation 2) (Dennis 1989; McCarthy 1997) to represent mate-finding success, and the Beverton-Holt to impose compensation, produces the function (Fig. 8c):

$$(33) \quad R = \frac{S}{\frac{1}{p} + \frac{S}{c}} \left[1 - \exp\left(-\frac{\ln(0.5)}{h} S\right) \right]$$

Here *h* is the density at which recruitment is half of that expected for the curve without depensation. Another model that could be explained using this approach is the un-normalised gamma function (Quinn II and Deriso 1999) (Fig. 8c):

$$(34) \quad R = aS^d e^{-bS}$$

This can be interpreted as a compensatory stage represented by the Ricker function and a depensatory stage modelled by the power function S^{d-1} .

Model choice

There are many ways in which depensation can be added to a population dynamics model. The choice will be dependent on the details specific to the population that is being modelled. When the depensatory and compensatory mechanisms regulating a population are poorly understood, model choice rests more on simplicity, flexibility, and the ability of the model to describe the available data. The models described above should provide a rich family of flexible curves from which to choose, as well as a template for constructing others.

Implications of depensation

The presence of depensation has implications in many different areas. These include endangered species management (Lamont *et al.* 1993; Groom 1998; Sinclair *et al.* 1998), reintroduction efforts (Sinclair *et al.* 1998), pest control (Knipling 1955), biological control (Hopper and Roush 1993; Grevstad 1999), optimal harvest policy (Peterman 1977; Clark 1985; Appeldoorn 1990; Botsford *et al.* 1993; Spencer and Collie 1997), spatial and temporal patterns in density (Steele and Henderson 1984; Kunin 1992; Lamont *et al.* 1993; Lewis and Kareiva 1993) and population genetics (Asmussen 1979; Hopf and Hopf 1985).

Reduced survival or fecundity at low densities (depensation) increases the probability of extinction. This threat has been brought up in the context of fragmented plant populations (Lamont *et al.* 1993; Groom 1998), primates (Swart *et al.* 1993), Salmonids (Parkinson 1990; Montgomery *et al.* 1996) and many other populations (for example see Fowler and Baker 1991). Because typically little is known about a population's dynamics at low densities, it is common to carry out population viability analyses using a quasi-extinction level in place of actual extinction (Ginzburg *et al.* 1982). This sidesteps the potential difficulties involved in modelling low density populations and as a consequence does not provide true extinction risks. Even defining quasi-extinction becomes difficult when dealing with species such as chinook salmon

(*Oncorhynchus tshawytscha*, Salmonidae) (Botsford and Brittnacher 1998) for which only a portion of the population is observed each year.

When populations are already at levels where depensation occurs, an understanding of the degree of depensation and its mechanism may be necessary for recovery. For example, populations facing depensatory predation may not be able to rebuild unless the predators are suppressed or the population is boosted above a threshold level. In a graphical analysis of several marsupial reintroductions in Australia, Sinclair *et al.* (1998) showed that for many of these failed attempts the data supported the hypothesis that the populations were subject to depensatory predation. Based on this analysis, they suggested a number of ways in which the effects of predation on these populations could be reduced, including predator control and habitat modification. Raveling (1989) came to similar conclusions about the management of the black brant (*Branta bernicla nigricans*, Anatidae) in Alaska where higher predation was observed for smaller colonies.

Harvest has the potential to reduce an otherwise robust population to a level where the negative effects of depensation become important (Clark 1985). In fact, Peterman (1977) showed that for a plausible case of depensatory salmon dynamics, even when using a common management goal such as maximum sustainable yield '... exploitation rates are inevitably close to the rates that would cause a drastic decrease in the population.' However, Grout (1993) and Liermann (1999) found that the estimated optimal harvest for many Pacific salmon populations does not change significantly when depensation is accounted for (except for severely depleted populations (Grout 1993). Botsford *et al.* (1993) assert that sea urchins in California have been so heavily exploited that densities are falling below threshold levels determined through experimentation. The potential for similar problems for the harvest of gastropods in tropical waters has been suggested (Appeldoorn 1990).

When the goal is to eradicate a species such as a pest or disease, depensatory dynamics can be beneficial. If a pest exhibits critical depensation then active reduction of the population is only necessary until the population has been reduced below the critical density (e.g. May 1977). In Milne's (1950) study of sheep ticks for example, reduced probability of mate finding at low densities imposed a lower limit below which the population could not survive.

The distribution of a population in space can influence the effects of depensation. This is especially true for sedentary species such as plants. Lamont *et al.* (1993) and Kunin (1992) both showed a decrease in reproductive success for smaller plant populations. As Lamont points out, the human tendency to fragment and reduce habitat when combined with depensatory dynamics significantly increase the probability of species extinction. This same situation exists for animal species where subpopulations become increasingly isolated on shrinking islands of suitable habitat. A mathematical analysis of territorial species led Lande (1987) to conclude that '... difficulty in finding a mate not only increases the minimum proportion of suitable habitat in a region necessary to sustain a stable population, but also creates an Allee effect.' Depensation has also been implicated in reduced rates of spread in invading populations. Lewis and Kareiva (1993) use a partial differential equation model of diffusion, that incorporates an Allee effect, to demonstrate that depensation may '... substantially reduce the rate at which the invader moves into a new environment.' Using an integro-difference equation Veit and Lewis (1996) support this idea by comparing the spread of the house finch (*Carpodacus mexicanus*, Fringillidae) in the United States to a model incorporating the Allee effect.

Depensation can produce unexpected temporal patterns as well. Many pelagic fish populations have experienced rapid changes in abundance separated by about 50-year periods of apparent stability. Based on the assumption that these stocks were alternating between two stable equilibria, Steele and Henderson (1984) subjected a depensatory model with two stable equilibria to environmental stochasticity with variance that increased with time period (red noise). When parameterised with estimates from two different stocks, the model produced patterns that mimicked the observed population fluctuations. Ludwig *et al.* (1978) and May (1977) describe how episodic outbreaks of the spruce budworm can be explained using a depensatory model. By modelling the forest's growth and response to the budworm infestation, they were able to produce dynamics where the budworm population occasionally jumped to an infestation equilibrium from the lower stable equilibrium which was maintained between outbreaks.

The wide-ranging implications of depensation emphasise the importance of considering the possibility of depensation when studying popula-

tions that are currently at, or may be reduced to, low densities.

Acknowledgements

We would like to thank Robert Francis, Nicolle Mode, Ashley Steel, Vern Liermann and three anonymous referees for reading through drafts of this manuscript and providing many useful editorial and content related suggestions.

References

- Allaine, D. (1991) The effects of colony size and breeding stage on colony defense pattern in the black-headed gull. *Acta Oecologica* **12**, 385–396.
- Allee, W.C. (1938) *The Social Life of Animals*. W. W. Norton Inc, New York.
- Allee, W.C., Emerson, A.E., Park, O., Park, T. and Schmidt, K.P. (1949) *Principles of animal ecology*. W B. Saunders Co., Philadelphia, PA.
- Andrewartha, H.G. and Birch, L.C. (1954) *The Distribution and Abundance of Animals*. The University of Chicago Press, Chicago.
- Appeldoorn, R.S. (1995) Potential depensatory mechanisms operating on reproductive output in gonochoristic molluscs, with particular reference to strombid gastropods. In: *Shellfish Life Histories and Shellfishery Models* (Moncton, New Brunswick, 25 June–29 June, 1990). D.E. Aiken, S.L. Waddy and G.Y. Conan, eds. ICES, Copenhagen, Denmark, pp. 13–18.
- Asmussen, M.A. (1979) Density-dependent selection II. the Allee effect. *American Naturalist* **114**, 796–809.
- Avilés, L. and Tufiño, P. (1998) Colony size and individual fitness in the social spider *Anelosimus eximius*. *American Naturalist* **152**, 403–418.
- Beverton, R.J.H. and Holt, S.J. (1957) *On the Dynamics of Exploited Fish Populations*, (Fishery Investigations, London Series 2, 19). UK Ministry of Agriculture and Fisheries, London.
- Bilby, R.E., Fransen, B.R. and Bisson, P.A. (1996) Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: Evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 164–173.
- Birkhead, T.R. (1977) The effect of habitat and density on breeding success in the common guillemot (*Uria aalge*). *Journal of Animal Ecology* **46**, 751–764.
- Bjorkstedt, E.P. (2000) Stock-recruitment relationships for life cycles that exhibit concurrent density dependence. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 459–467.
- Botsford, L.W., Brittnacher, J.G. (1998) Viability of Sacramento River winter-run chinook salmon. *Conservation Biology* **12**, 65–79.

- Botsford, L.W., Quinn, J.F., Wing, S.R. and Brittnacher, J.G. (1993) Rotating spatial harvest of a benthic invertebrate, the red sea urchin, *Strongylocentrotus franciscanus*. In: *Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations* (Anchorage, Alaska, 21 October-24 October, 1993). G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke and T.J. Quinn, II, eds. Alaska Sea Grant College Program, Fairbanks, Alaska, pp. 409–428.
- Boyd, S.K. and Blaustein, A.R. (1985) Familiarity and inbreeding avoidance in the gray-tailed vole (*Microtus canicaudus*). *Journal of Mammalogy* **66**, 348–352.
- Brock, V.E. and Riffenburgh, R.H. (1963) Fish Schooling: a possible factor in reducing predation. *Journal du Conseil International pour l'Exploration de la Mer* **25**, 307–317.
- Cederholm, C.J., Kunze, M.D., Murota, T. and Sibatani, A. (1999) Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* **24**, 6–15.
- Clark, C.W. (1985) *Bioeconomic Modelling and Fisheries Management*. John Wiley & Sons, New York, NY.
- Clutton-Brock, T.H., Gaynor, D., McIlrath, B.M., Maccoll, A.D.C., Kansky, R., Chadwick, P., Manser, M., Skinner, J.D. and Brotherton, P.N.M. (1999) Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology* **68**, 672–683.
- Collie, J.S. and Spencer, P.D. (1993) Management strategies for fish populations subject to long-term environmental variability and depensatory predation. In: *Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations* (Anchorage, Alaska, 21 October-24 October, 1993). G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke and T.J. Quinn, II, eds. Alaska Sea Grant College Program, Fairbanks, Alaska, pp. 629–650.
- Courchamp, F., Clutton-Brock, T. and Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* **14**, 405–410.
- Creel, S. and Creel, N.M. (1995) Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour* **50**, 1325–1339.
- Crittenden, R.N. (1994) A model for the processes regulating recruitment for a sockeye salmon stock. *Ecological Modelling* **71**, 1–3.
- DeAngelis, D.L., Christensen, S.W. and Clark, A.G. (1977) Responses of a fish population model to young-of-the-year mortality. *Journal of the Fisheries Research Board of Canada* **34**, 2124–2132.
- Dennis, B. (1989) Allee effects: population growth, critical density, and the chance of extinction. *Natural Resource Modeling* **3**, 481–538.
- Emlen, J.M. (1984) *Population biology. The Coevolution of Population Dynamics and Behaviour*. Macmillan, New York, NY.
- Emslie, S.D., Karnovsky, N. and Trivelpiece, W. (1995) Avian predation at penguin colonies on King George Island, Antarctica. *Wilson Bulletin* **107**, 317–327.
- Errington, P.L. (1940) Natural restocking of mustkrat-vacant habitats. *Journal of Wildlife Management* **4**, 173–185.
- Fowler, C.W. and Baker, J.D. (1991) A review of animal population dynamics at extremely reduced population levels. *Report of the International Whaling Commission* **41**, 545–554.
- Frank, K.T. and Brickman, D. (2000) Allee effects and compensatory population dynamics within a stock complex. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 513–517.
- Fresh, K.L. and Schroder, S.L. (1987) Influence of the abundance, size and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 236–243.
- Ginzburg, L.R., Slobodkin, L.B., Johnson, K. and Bindman, A.G. (1982) Quasiextinction probabilities as a measure of impact on population growth. *Risk Analysis* **21**, 171–181.
- Grevstad, F.S. (1999) Factors influencing the chance of population establishment: Implications for release strategies in biocontrol. *Ecological Applications* **9**, 1439–1447.
- Groom, M.J. (1998) Allee effects limit population viability of an annual plant. *American Naturalist* **151**, 487–496.
- Grout, J.A. (1993) An evaluation of the management implications of depensatory predation mortality in Pacific salmon using Bayesian analysis. MS Thesis, Simon Fraser University, 71 pages.
- Hassell, M.P. (1978) *The Dynamics of Arthropod Predator-Prey Systems* (Monographs in Population Biology Vol. **13**). Princeton University Press, Princeton, New Jersey.
- Hassell, M.P., Lawton, J.H. and Beddington, J.R. (1977) Sigmoid functional responses by invertebrate predators and parasitoids. *Journal of Animal Ecology* **46**, 249–262.
- Hilborn, R. and Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment. Choice, Dynamics and Uncertainty*. Chapman & Hall, New York.
- Holling, C.S. (1959a) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* **91**, 293–320.
- Holling, C.S. (1959b) Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* **91**, 385–398.
- Holling, C.S. (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* **45**, 1–60.
- Hopf, F.A. and Hopf, F.W. (1985) The role of the Allee effect in species packing. *Theoretical Population Biology* **27**, 27–50.
- Hopper, K.R. and Roush, R.T. (1993) Mate finding, dispersal, number released, and the success of biological control introductions. *Ecological Entomology* **18**, 321–331.
- Hutchings, J.A. and Myers, R.A. (1994) What can be learned from the collapse of a renewable resource?

- Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2126–2146.
- Hvidsten, N.A. and Johnsen, B.O. (1993) Increased recapture rate of adult Atlantic salmon released as smolts into large shoals of wild smolts in the River Orkla, Norway. *North American Journal of Fisheries Management* **13**, 272–276.
- Ivlev, V.S. (1961) *Experimental Ecology of the Feeding of Fishes*. Yale University Press, New Haven.
- Jacobs, J. (1984) Cooperation, optimal density and low density thresholds: yet another modification of the logistic model. *Oecologia* **64**, 389–395.
- Knipling, E.B. (1955) Possibilities of insect control or eradication through the use of sexually sterile males. *Journal of Economic Entomology* **48**, 459–462.
- Kunin, W. (1992) Density and reproductive success in wild populations of *Diplotaxis eruroides* (Brassicaceae). *Oecologia* **91**, 129–133.
- Kuussaari, M., Saccheri, I., Camara, M. and Hanski, I. (1998) Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos* **82**, 384–392.
- Lamont, B.B., Klinkhamer, P.G.L. and Witkowski, E.T.F. (1993) Population fragmentation may reduce fertility to zero in *Banksia goodii* – A demonstration of the Allee effect. *Oecologia* **94**, 446–450.
- Lande, R. (1987) Extinction thresholds in demographic models of territorial populations. *American Naturalist* **130**, 624–635.
- Lande, R., Engen, S. and Saether, B.E. (1994) Optimal harvesting, economic discounting and extinction risk in fluctuating populations. *Nature* **372**, 88–90.
- Landeau, L. and Terborgh, J. (1986) Oddity and the 'confusion effect' in predation. *Animal Behaviour* **34**, 1372–1380.
- Larkin, P.A. (1971) Simulation studies of the Adams River sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* **28**, 1493–1502.
- Larkin, P.A., Raleigh, R.F. and Wilimovsky, N.J. (1964) Some alternative premises for constructing theoretical reproductive curves. *Journal of the Fisheries Research Board of Canada* **21**, 477–484.
- Larkin, G.A. and Slaney, P.A. (1997) Implications of trends in marine-derived nutrient influx to south coastal British Columbia Salmonid production. *Fisheries* **22**, 16–24.
- Lawes, M.J. and Kirkman, S. (1996) Egg recognition and interspecific brood parasitism rates in red bishops (*Aves: Ploceidae*). *Animal Behaviour* **52**, 553–563.
- Leopold, A. (1933) *Game Management*. Scribner's sons, New York.
- Levitan, D.R., Sewell, Mary, A. and Fu, S.C. (1992) How distribution and abundance influence fertilization success. *Ecology* **73**, 248–254.
- Lewis, M.A. and Kareiva, P. (1993) Allee dynamics and the spread of invading organisms. *Theoretical Population Biology* **43**, 141–158.
- Liermann, M. (1999) *Depensation: Evidence and Implications*. PhD Thesis, University of Washington, 111 pages.
- Liermann, M. and Hilborn, R. (1997) Depensation in fish stocks: a hierarchical Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1976–1984.
- Ludwig, D., Jones, D.D. and Holling, C.S. (1978) Qualitative analysis of insect outbreak systems: The spruce budworm and forest. *Journal of Animal Ecology* **47**, 315–332.
- Marsh, A.C. and Ribbink, A.J. (1986) Feeding schools among Lake Malawi cichlid fishes. *Environmental Biology of Fishes* **15**, 75–79.
- Mathisen, O.A. (1972) Biogenic enrichment of sockeye salmon lakes and stock productivity. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **18**, 1089–1095.
- May, R. (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* **269**, 471–477.
- McCarthy, M.A. (1997) The allee effect, finding mates and theoretical models. *Ecological Modelling* **103**, 99–102.
- Milne, A. (1950) The ecology of the sheep tick, *Ixodes ricinus* L. *Parasitology* **40**, 35–45.
- Montgomery, D.R., Buffington, J.M., Peterman, N.P., Schuett-Hames, D. and Quinn, T.P. (1996) Salmonid modifications of gravel streambeds: implications for bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 1061–1070.
- Murdoch, W.W. (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* **39**, 335–354.
- Myers, R.A., Barrowman, N.J., Hutchings, J.A. and Rosenberg, A.A. (1995) Population dynamics of exploited fish stocks at low population levels. *Science* **269**, 1106–1108.
- Neave, F. (1953) Principles affecting the size of pink and chum salmon populations in British Columbia. *Journal of the Fisheries Research Board of Canada* **9**, 450–491.
- Nehlsen, W., Williams, J. and Lichatowich, J. (1991) Pacific salmon at the Crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* **16**, 21.
- 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.
- Norris, K. and Johnstone, I. (1998) The functional response of oystercatchers (*Haematopus ostralegus*) searching for cockles (*Cerastoderma edule*) by touch. *Journal of Animal Ecology* **67**, 329–346.
- Odum, H.T. and Allee, W.C. (1954) A note on the stable point of populations showing both intraspecific cooperation and disoperation. *Ecology* **35**, 95–97.
- Park, T. (1933) Studies in population physiology. II. Factors regulating initial growth of *Tribolium confusum* populations. *Journal of Experimental Zoology* **65**, 17–42.
- Parkinson, E.A. (1990) Impaired school formation at low density: A mechanism for depensatory mortality in

- sockeye salmon. *B. C. Fisheries Branch, Fisheries Management Report* **no. 99**, 1–17.
- Parrish, R.H. and MacCall, A.D. (1978) Climatic variation and exploitation in the pacific mackerel fishery. *California Department of Fish and Game, Fish Bulletin* **167**, 110 pp.
- Peterman, R.M. (1977) A simple mechanism that causes collapsing stability regions in exploited salmonid populations. *Journal of the Fisheries Research Board of Canada* **34**, 1130–1142.
- Peterman, R.M. (1980) Dynamics of native Indian food fisheries on salmon in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 561–566.
- Peterman, R.M. and Gatto, M. (1978) Estimation of functional responses of predators on juvenile salmon. *Journal of the Fisheries Research Board of Canada* **35**, 797–808.
- Porter, J.M. (1990) Patterns of recruitment to the breeding group in the kittiwake *Rissa tridactyla*. *Animal Behaviour* **40**, 350–360.
- Prout, T. and McChesney, F. (1985) Competition among immatures affects their adult fertility: population dynamics. *American Naturalist* **126**, 521–558.
- Quinn II, T.J. and Deriso, R.B. (1999). *Quantitative Fish Dynamics*. Oxford University Press, New York.
- Raveling, D.G. (1989) Nest-predation rates in relation to colony size of black brant. *Journal of Wildlife Management* **53**, 87–90.
- Real, L.A. (1977) The kinetics of functional response. *American Naturalist* **111**, 289–300.
- Ricker, W.E. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada* **11**, 559–623.
- Ricker, W.E. (1997) Cycles of abundance among Fraser River sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 950–968.
- Robertson, T.B. (1921) Experimental studies on cellular reproduction. II. The influence of mutual contiguity upon reproductive rate and the part played therein by the 'X substance' in bacterised infusions which stimulates the multiplication of Infusoria. *Biochemical Journal* **15**, 612–619.
- Rood, J.P. (1990) Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Animal Behaviour* **39**, 566–572.
- Royama, T. (1970) Factors governing the hunting behaviour and selection of food by the great tit, *Parus major* L. *Journal of Animal Ecology* **39**, 619–668.
- Royama, T. (1971). *A Comparative Study of Models for Predation and Parasitism*, (Researches on population ecology Suppl. 1). The Society of Population Ecology, Entomological Laboratory, Kyoto, Japan.
- Ruggerone, G.T. and Rogers, D.E. (1984) Arctic char predation on sockeye salmon smolts at Little Togiak River, Alaska. *Fishery Bulletin* **82**, 401–410.
- Sæther, B.-E., Ringsby, T.H. and Roskaft, E. (1996) Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos* **77**, 217–226.
- Scarff, J.E. (1977a) The international management of whales, dolphins and porpoises: an interdisciplinary assessment. Part I. *Ecological Law Quarterly* **6**, 323–426.
- Scarff, J.E. (1977b) The international management of whales, dolphins and porpoises: an interdisciplinary assessment. Part II. *Ecological Law Quarterly* **6**, 571–638.
- Shelton, P.A. and Healey, B.P. (1999) Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1521–1524.
- Sinclair, A.R.E. (1989) Population Regulation in Animals. In: *Ecological Concepts: the Contribution of Ecology to an Understanding of the Natural World*, (ed. J.M. Cherrett). 29th symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford, pp. 197–241.
- Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P. and Newsome, A.E. (1998) Predicting effects of predation on conservation of endangered prey. *Conservation Biology* **12**, 1–13.
- Sjöberg, S. (1980) Zooplankton feeding and queueing theory. *Ecological Modelling* **10**, 215–225.
- Spencer, P.D. and Collie, J.S. (1997) Effect of nonlinear predation rates on rebuilding the Georges Bank haddock (*Melanogrammus aeglefinus*) stock. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 2920–2929.
- Stamou, G.P. and Asikidis, M.D. (1989) The effect of density on the demographic parameters of two oribatid mites. *Revue d'Ecologie et de Biologie Du Sology* **26**, 321–330.
- Steele, J. and Henderson, E. (1984) Modeling long-term fluctuations in fish stocks. *Science* **224**, 985–987.
- Stephens, P.A., Sutherland, W.J. and Freckleton, R.P. (1999) What is the Allee effect? *Oikos* **87**, 185–190.
- Swart, J., Lawes, M.J. and Perrin, M.R. (1993) A mathematical model to investigate the demographic viability of low-density samango monkey (*Cercopithecus mitis*) populations in Natal, South Africa. *Ecological Modelling* **70**, 3–4.
- Thompson, G.G. (1993) A proposal for a threshold stock size and maximum fishing mortality rate. In: *Risk Evaluation and Biological Reference Points for Fisheries Management* (eds S.J. Smith, J.J. Hunt and D. Rivard). Canadian Special Publication of Fisheries and Aquatic Sciences Vol. 120. Fisheries and Oceans Canada, Ottawa, 303–320.
- Tinbergen, L. (1960) The natural control of insects in pinewoods, 1: factors influencing the intensity of predation by song birds. *Archives Neerlandaises de Zoologie* **13**, 266–336.
- Tonkyn, D.W. (1986) Predator-mediated mutualism: theory and test in the Homoptera. *Journal of Theoretical Biology* **118**, 15–31.
- Veit, R.R. and Lewis, M.A. (1996) Dispersal, population growth, and the allee effect: Dynamics of the house finch invasion of eastern North America. *American Naturalist* **148**, 255–274.

- Walters, C. and Kitchell, J.F. (2001) Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 39–50.
- Watt, K.E.F. (1959) A mathematical model for the effect of densities of attacked and attacking species on the number of attacked. *Canadian Entomologist* **91**, 129–144.
- Wilbur, H.M. (1977) Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. *Ecology* **58**, 196–200.
- Wood, C.C. (1987) Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. 1: Predation during the seaward migration. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 941–949.