Influence of rare ecological events on pinniped social structure and population dynamics

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Synopsis

The best documented 'rare' ecological events affecting pinniped populations are (1) drastic changes in physical parameters and food resources, e.g. during the 1982–83 El Niño event in the eastern Pacific, and (2) disease outbreaks such as the 1988 epizootic caused by phocine distemper virus in harbour seals. These events were particularly drastic, but smaller events seem to occur quite regularly, if unpredictably. Such events are part of the environmental variance to which most animals are exposed during their lifetime and they may have significant consequences for social and population processes or structure. El Niños can also serve as models of the potential reaction of top predators to human-induced global changes.

During both the 1982–83 El Niño and the epizootic, social patterns changed in response to reduced competition for space and food in the declining pinniped populations. Mother–young interactions and interactions among both females and males were altered, and animals were redistributed over the available habitat. Dispersal, mortality and fertility changed in the affected populations. The magnitude of the effects on sex, cohorts and (sub-) populations depended on the timing of the event in relation to the annual life cycle of the animals.

Rare events may influence differentiation among populations and reduce the long-term mean carrying capacity of the environment and/or the probability of reaching the carrying capacity. They also may create bottlenecks, thereby reducing population heterozygosity. The split of populations into more or less separated subpopulations decreases the probability of extinction. Density-dependent factors are known to influence pinniped population dynamics, but environmental stress as a density-independent, stochastic process influences the population dynamics of mammals as large as pinnipeds far more than is generally appreciated.

Introduction

... and there shall be famines, and pestilences, and earthquakes, in various places (Matthew 24:7)

One of the major problems in ecology is the explanation of distribution, abundance and persistence of populations. The debate about the causes of population persistence and relative stability (DeAngelis & Waterhouse 1987) has become ever more important as conservation of species has become a more pressing need (Simberloff 1988). The relative importance of density-dependent regulative processes and density-independent stochastic events for the determination of population size is still an unresolved issue. Generally, populations of larger animals (in particular larger vertebrates) are believed to be less influenced by stochastic events than populations of small animals (e.g. insects).

Within the last decade, two apparently stochastic events of catastrophic dimension befell pinniped populations: one was the Pacific-wide El Niño in 1982–83, the other the harbour seal (*Phoca vitulina*) epizootic of 1988–89 in the North Sea. Both these events had a major impact on pinniped populations and both were documented in detail. They can serve as examples of the influence of rare ecological events on pinniped populations and may help to elucidate the role of stochastic processes for population dynamics of large vertebrates. Since detailed documentation of these events is impossible in the space available here and has been provided elsewhere (Trillmich & Ono 1991; Dietz, Heide-Jorgensen & Härkönen 1989; Heide-Jorgensen *et al.* 1992), this paper will concentrate on a number of more general issues.

First, methodological problems of the definition of a 'rare' event and of the documentation of its effects will be briefly discussed. Keeping these problems in mind, examples will then be given of how physical or biological stressors influence the main population parameters, i.e. mortality, fertility and migration/dispersal, and how these effects differ between the sexes and among age classes. Wherever possible, the more poorly documented role that behavioural factors play in mediating the population effects will be mentioned. Finally, the role that spatial heterogeneity and differences in timing of major stochastic environmental disturbances play in long-term population survival will be discussed.

What are rare ecological events?

The definition of a 'rare ecological event' depends largely on one's time frame. A rather vague definition would be 'an event of major impact on population structure or abundance'. 'Rare' positive events producing a

boom in population condition and subsequent reproduction have never been described for pinnipeds. However, the reduction of whale populations in the Southern Ocean may have been a rare environmental effect allowing the phenomenal rates of increase realized by the Antarctic fur seal (*Arctocephalus gazella*) population after the end of sealing (Croxall *et al.* 1988). La Niña, very cold, productive years after the warm-water catastrophes of El Niño, may provide another example of a rare positive event (see below).

Weatherhead (1986) studied the frequency of reports about unusual events. He relied on the investigators to know what was 'unusual' for their study system. Most 'unusual' events were abiotic in nature (87%) and, surprisingly, the frequency with which they were recorded declined in studies which spanned more than seven years. Apparently, what is considered rare or unusual changes somewhat with an investigator's experience in a particular study system. For Weatherhead's sample of studies on mammals of temperate and tropical ecosystems ($n = 37$), 8% reported unusual events and Weatherhead concluded from this that 'rare' ecological events are relatively frequent. Rare biotic events, in particular diseases, may be under-represented in his samples since they are harder to diagnose than abiotic changes for which weather reports often provide the evidence.

For the purpose of this paper rare ecological events are loosely defined as environmental stressors which induce major deviations of birth, death, or migration rate in one or several age/sex classes away from long-term means. The events have an influence on population structure and/or population dynamics for several subsequent years.

Such changes may be mediated primarily by abiotic factors like temperature or oceanic regime (as in the El Niño example), or by biotic factors, e.g. new parasites as in the case of the harbour seal epizootic.

Methodological problems

Census methods

Given that a rare ecological event is taking place, it is a far from trivial matter to determine population changes in the affected pinniped popu-lation(s). Most population assessments produce only relative numbers or indices of population size, whereas the real changes in numbers are needed to quantify the effects of an event. Data are also required to assess the impact of an event on different age and sex classes. Such detail is particularly important in assessing the long-term consequences of an event.

Pinnipeds are usually distributed over wide, often inaccessible areas, which makes a census of the desired accuracy problematic. Aerial censuses may often be the best tool, but they still provide only an index of
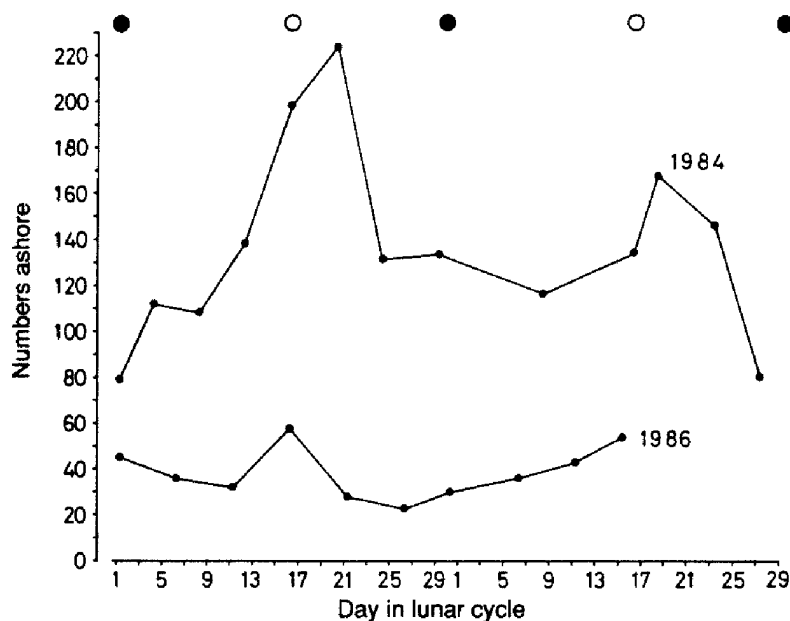
Fig. 1. Numbers of Galapagos fur seals ashore over the lunar cycle. Day 1 and 29 correspond to new moon, day 16 to full moon (see symbols above graph). The 1984 censuses were made between August 26 and October 18 during the cold season when fur seals reproduce. At this time, females spend on average about 60% of their time ashore. The 1986 censuses were made between March 10 and April 23 during the warm season, when females spend only about 20% of the time ashore.

abundance, as many seals will be at sea during the census. Furthermore, the proportions of the populations ashore vary considerably depending upon time of day, phase of the lunar cycle and season (Trillmich & Mohren 1981; Thompson & Harwood 1990; Fig. 1). To estimate population size and its changes for pinnipeds, a thorough study of behaviour over the tidal, daily, lunar, seasonal, and life cycles is needed before census numbers can be converted into population estimates that are at all reliable.

The importance of such studies for the assessment of population change was illustrated by the 1988 epizootic among harbour seals of the Wadden Sea where mortality from carcass counts was 108% of the population estimate for the Wadden Sea before the event (Dietz et al. 1989; Fig. 2). Consequently, numbers counted in aerial surveys prior to the epizootic did not represent 100% of the population, although additional biases may have resulted from a redistribution of seal carcasses (Heidemann & Schwarz 1990; Reijnders 1989; Reijnders, Ries & Traut 1990).

A complicating factor: habitat choice

In addition to the uncertainties surrounding most population estimates of pinnipeds, another factor complicates the correct assessment of population changes. During a population crash animals may move into the best habitat,
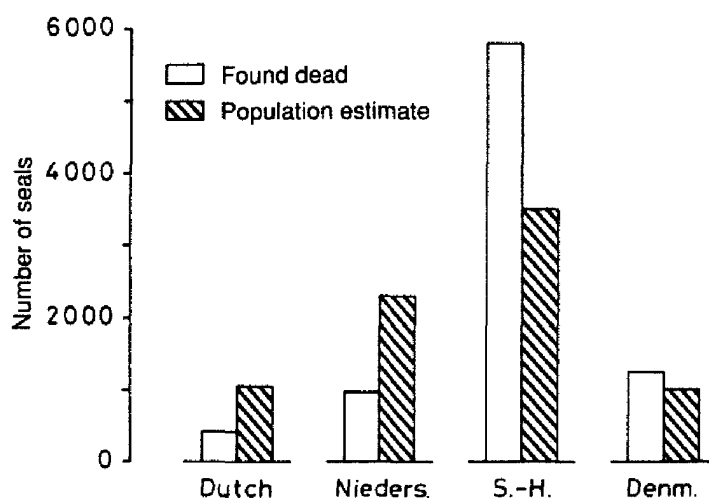
Fig. 2. Number of harbour seals found dead and previous population estimates for subsections of the Wadden Sea area (data from Dietz *et al.* 1989). Coast-section abbreviations: Dutch; Nieders. = Niedersachsen; S.-H. = Schleswig-Holstein; Denm. = Denmark.

making it appear almost as full as before the catastrophe. Such effects are expected to be widespread if individuals distribute according to an ideal free or despotic free distribution over the available habitat (Fretwell & Lucas 1970; Rosenzweig 1985; Milinski & Parker 1991). Estimates of population size in good habitat (where researchers tend to make their observations) will then underestimate the impact of an event.

Despite the reported high site fidelity of pinnipeds, such shifts among habitats of differing quality have been documented for several species. For example, in northern elephant seals (*Mirounga angustirostris*) about 32% of juvenile females gave birth away from their own birth site, and 17.6% of all females changed the location where they gave birth at least once in their lifetime (Le Boeuf & Reiter 1988). Apparently, dominant animals fill the best habitat first and less competitive (young) individuals settle elsewhere once the prime habitat is occupied. The approximation to a free distribution is normally achieved primarily by dispersal of young animals, but under catastrophic conditions all animals may take part.

The El Niño: a model event

El Niño (EN) is an unpredictably occurring but regular feature of the eastern tropical Pacific (Arntz, Pearcy & Trillmich 1991; Quinn, Neal & Antuñez de Mayolo 1987). Figure 3 shows the cumulative probability distribution of the intervals between events. Using a lognormal fit to these data Glynn (1988) determined that the mean recurrence interval for strong events was 11.95 years (± 6.6 S.D.) and for moderate events it was 6.1 (± 3.38) years. In view of the potential lifespan of an otariid pinniped (roughly
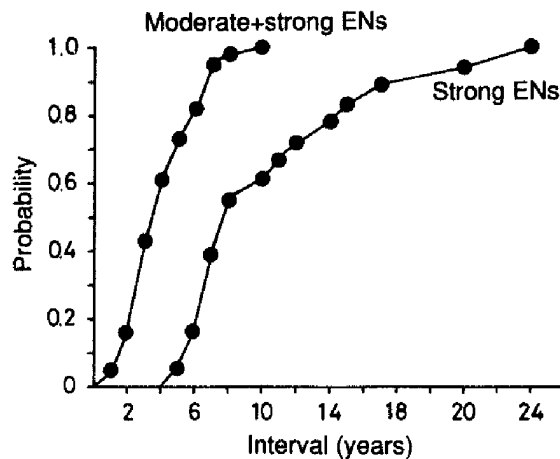
Fig. 3. Cumulative probability of a next moderate or strong, and a next strong El Niño after the end of a previous one (data from Quinn *et al.* 1987).

10–20 years), almost every animal surviving to reproductive age will experience such an event and most animals will even have to live through a strong event. In the long-term view, EN is an example of a regular, unpredictable event which may appear to be exceptional in a short study.

Biotic effects of EN

Marine ecosystems along the eastern margin of the Pacific are highly productive owing to the influence of cold currents and coastal upwellngs. El Niño-Southern Oscillation (ENSO, here called EN) refers to an oceanographic/meteorological condition causing massive advection of warm waters into the cold ocean current systems along the eastern margin of the tropical and subtropical Pacific. In very strong events, the influence of the disturbance is globally felt and influences coastal ecosystems Pacific-wide from Fireland to Alaska (Fahrbach, Trillmich & Arntz 1991, and references therein). During EN, productivity of the marine ecosystems decreases (but may increase towards subpolar latitudes), prey distributions and prey quality for pinnipeds decrease, and increased sea surface levels may cause inundation of otherwise safe haul-out and pupping sites.

These effects have been documented in detail for a number of species for the 1982–83 EN which was the strongest in the last 100 years (Trillmich & Ono 1991). Here, examples will be selected of changes caused by the disturbance. Since EN originates in the tropical Pacific all effects were generally strongest at the equator and attenuated towards higher latitudes. Later observations during other ENs demonstrated that effects observed during the strong 1982–83 EN at higher latitudes were similar to those caused by weaker ENs at low latitudes (Trillmich *et al.* 1991).

Mortality and consequent changes in age structure

By removing whole cohorts or even series of cohorts through mortality of pups and juveniles, EN 1982–83 caused a very ragged age structure in the affected populations. The most striking example of this effect is the case of the Galapagos fur seal in which all individuals of the 1980–82 cohorts died during EN (Trillmich & Limberger 1985; Trillmich & Dellinger 1991). However, loss of whole cohorts or major percentages of cohorts was also reported from the Galapagos sea lion (Trillmich & Dellinger 1991), the South American fur seal (*Arctocephalus australis*) and sea lion (*Otaria byronia*) in Peru (Majluf 1991), the California sea lion (*Zalophus c. californianus*) along the coast of California (Francis & Heath 1991a; DeLong *et al.* 1991), the northern fur seal (*Callorhinus ursinus*) on San Miguel Island (DeLong & Antonelis 1991), and the northern elephant seal (Le Boeuf & Reiter 1991; Huber, Beckham & Nisbet 1991; Stewart & Yochem 1991). Apparently there was no subsequent density-dependent compensation through increased survival of a small cohort; thus the contribution of the affected cohort to the total reproductive output of a population will be almost negligible, as is shown by data on the northern elephant seal (Fig. 4; Le Boeuf & Reiter 1991). Data on birds even show that in affected cohorts low initial survival might be coupled to survival rates which throughout life are lower than those of cohorts from more normal years (Gibbs & Grant 1987). Such effects of poor early rearing conditions on long-term 'quality' (fitness) of a cohort have not been documented for pinnipeds but could slow population recovery after an event.

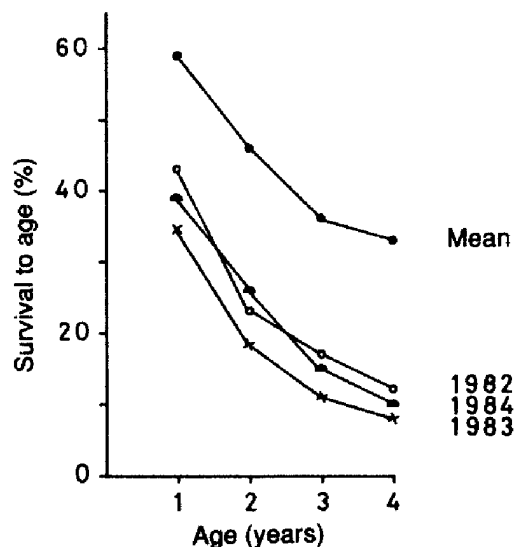Not only did fewer juveniles survive, but adults were also affected, and

Fig. 4. Survival of elephant seal cohorts was lower for pups weaned in 1982–84: mean = mean of years 1971 to 1981 (after data in Le Boeuf & Reiter 1991).

mortality in the eastern tropical Pacific pinniped populations increased significantly (Trillmich *et al.* 1991). During the 1982–83 EN, 50–70% of adult female Galapagos fur seals died and increased adult mortality was also documented for California sea lions (DeLong *et al.* 1991) and northern fur seals on San Miguel (DeLong & Antonelis 1991). This increased adult mortality affected males and females quite differently. Many males of the Galapagos fur seal and sea lion, as well as territorial males of the South American fur seal in Peru, died during and immediately after the EN, presumably because they had been fasting during the reproductive season and returned to the sea in poor condition at a time when food availability was minimal. In Galapagos, 100% of the territorial Galapagos fur seal males died in 1982 (Trillmich & Limberger 1985). In California sea lions, females apparently suffered relatively higher mortality than males as total female numbers on the Channel Islands had not recovered by 1986 whereas male numbers remained stable throughout. Apparently males had escaped to the north from the area of major EN impact (Huber 1991). Similarly, adult female northern fur seals on San Miguel Island appeared to suffer major mortality during EN whereas males showed no indication of a decrease (DeLong & Antonelis 1991). In northern elephant seals no obvious increase in adult female mortality was noticed and there was only a slight increase in male mortality.

Considering that differences in life history and ecology are almost as great between the pinniped sexes as between pinnipeds and other species, a differential impact of a catastrophic decline in food abundance is to be expected. This is the consequence of the great sexual dimorphism in size and behaviour which characterizes the polygynously breeding species. Unfortunately, no comparative data are available for less dimorphic species like harbour seals.

Fertility

Concomitant with changes in mortality, the 1982–83 EN caused major effects on female fertility. In Galapagos fur seals, only 11% of the normal pupping rate was observed after the end of EN in 1983. Northern fur seals on San Miguel Island were similarly affected, but here it was more difficult to disentangle the effects of female mortality from reduced pupping rate (DeLong & Antonelis 1991). Among California sea lions on the Channel Islands (Francis & Heath 1991a) and the outer coast of Mexico (Aurioles & Le Boeuf 1991) fertility was reduced to 30–70% of normal.

The elephant seals on Año Nuevo and the Farallones reacted differently to EN despite the fact that elephant seal females feed in the open ocean beyond the shelf break (see Le Boeuf *et al.* this volume; R. L. DeLong, B. S. Stewart & R. Hill, pers. comm.), an area which most probably was similarly affected during EN for both populations. Nevertheless, there was a

clear decrease in female fertility on the Farallones (Huber *et al.* 1991) and no noticeable change in fertility on Año Nuevo (Le Boeuf & Reiter 1991), suggesting that these animals feed in different patches of ocean.

In addition to immediate changes in fertility there was also a delayed effect on female fertility. Elephant seal cohorts that grew up under EN conditions delayed first reproduction (Le Boeuf & Reiter 1991; Huber *et al.* 1991).

The importance of movements and of spatial differences over the range of a population

Shifts in habitat may have reduced the impact of EN by improving survival chances of animals in the best available habitat. Galapagos fur seals concentrated into the best pupping habitats after EN 1982–83 whereas the coast around this colony was deserted (Trillmich & Dellinger 1991). Similarly, California sea lions shifted among the Channel Islands (DeLong *et al.* 1991).

Some South American fur seals escaped the worst impact of EN by migrating away from the highly disturbed Peruvian upwelling system. They emigrated into northern Chile during 1982, where many eventually settled permanently and bred (Guerra & Portflitt 1991).

In California, northern fur seal juveniles apparently migrated further north than in normal years, even producing the first record of an animal from San Miguel Island back on the Pribilof Islands (DeLong & Antonelis 1991). California sea lion males and juveniles migrated in greater numbers to central California in 1983 and 1984 (Huber 1991) than in other years, thus avoiding the greater EN impact in the Channel Island area of southern California. Adult females were restricted in their capacity to move out of affected areas because of the need to return to pups ashore. This may explain why their mortality increased more than that of males and their fertility was lower in the year(s) following the 1983 EN impact in California (Francis & Heath 1991a; DeLong *et al.* 1991).

Sheltered subpopulations may contribute to long-term population persistence. Interestingly, the Sea of Cortez subpopulation of the California sea lion showed no influence of EN (Aurioles & Le Boeuf 1991), whereas the population just outside the Gulf which depends on upwelling processes for its food resources was affected just as much as all other animals along the Californian coast.

On the Galapagos, the northern population of the fur seal on Genovesa came close to extinction. Before EN, in 1978, it was estimated at approximately 1000 individuals, but after EN censuses in 1988 and 1989 showed that the population had been reduced to between 10% and 20% of its former size (F. Trillmich & B. J. Le Boeuf unpubl. data). Compared to this, the population on the western Islands declined by about 50%.

Both these cases demonstrate that spatial differentiation can decrease the probability of species extinction because a subpopulation sheltered in a habitat less affected by El Niño can repopulate more severely affected areas.

Maternal behaviour

Females were clearly energy-stressed during EN. This applied to both otariids and the elephant seals. Elephant seal females stayed at sea for significantly longer periods between the end of lactation and the onset of the moult. Apparently they needed more time to recover from the stress of lactation under poor foraging conditions. While lactating on land, however, these animals only suffered from the immediate effects of storms which caused increased pup mortality (Le Boeuf & Reiter 1991; Huber et al. 1991; Stewart & Yochem 1991); they showed no signs that they were providing less food for the pups.

In contrast, otariid pinniped mothers, which forage during pup-rearing, needed more time and energy to replenish their reserves during foraging trips to sea. They showed more diving activity at sea to get the same food intake (Feldkamp, DeLong & Antonelis 1991; Costa, Antonelis & DeLong 1991) and spent more time away from their young (Heath et al. 1991). Consequently pups received less food and in many cases starved (Boness, Oftedal & Ono 1991; Iverson, Oftedal & Ono 1991). In the California sea lion, pups reduced their energy expenditure but this was not sufficient to make up for reduced milk intake when mothers were ashore (Ono & Boness 1991). Slower growth of juveniles then led to longer times to weaning, which was most pronounced in male young (Francis & Heath 1991b). Galapagos fur seal mothers proved totally unable to support the energetic demands of their pups and abandoned them.

Effects on intraspecific competition

Following the decrease in male numbers, the territorial system of Galapagos fur seals changed to a dominance system, since only very few large males were still alive after EN (Trillmich & Limberger 1985). These males claimed large areas but were unable to defend them against smaller intruding males. Reduced competition among males thus led to a major change in social pattern. The loss of three entire Galapagos fur seal cohorts and reduction of those from 1979 and 1983 may lead to similar changes about 8–10 years after the event when most males from these cohorts are expected to breed. These changes in the population's age structure will lead to reduced sexual selection through male–male competition on the cohorts which mature immediately after a major event and another set of cohorts 8–10 years later. Reduced competition within and between the sexes will reduce density-dependent effects on females. This will aid recovery of the population by

decreasing age at first reproduction, increasing birth rate, and reducing mortality of pups, juveniles and perhaps adult females alike (Fowler 1990).

Weaker events and rare positive events

Weak events have much lesser effects on otariid populations in the eastern tropical Pacific (Majluf 1991). Rather than causing increased mortality, they lead to delayed weaning of young, which are very likely to be suckled into their second year of life. This lengthened lactation decreases female fertility (Trillmich 1990) and could periodically decrease population growth rate.

Another factor complicating the analysis of the effects of EN events on pinniped populations is the so-called 'La Niña'. After EN, sea surface temperatures regularly decline below the long-term mean and marine productivity increases above the mean. The effect was very strong in 1984 and 1985 in the tropical Pacific when the usual warm season on Galapagos was almost undetectable. Consequently, young Galapagos fur seals and sea lions grew extraordinarily fast and almost all young were independent of their mothers at one year of age. In addition, these cohorts have grown particularly fast and are likely to begin reproduction earlier than other cohorts. Such an upswing of recruitment rate following an EN clearly reduces the impact of the environmental disturbance.

The effects of diseases

Biotic disturbances represent the other major type of environmental stress. The recent harbour seal epizootic in the North Sea area is a good example. Diseases influence populations differently from abiotic factors mainly because transmission dynamics and development of resistance play a key role (Anderson 1991).

Frequency of diseases

Over the last 100 years epizootics have been reported for several species of seals. These have been compiled by Dietz et al. (1989), Harwood & Hall (1990) and Heide-Jorgensen et al. (1992) and are listed in Table 1. Diseases were observed on all continents, except Australia, and also appear to be recurrent events in some pinniped populations. The technical problems of investigating the occurrence and distribution of disease-related mortality in wild populations of pinnipeds are still formidable and explain why we have information only about mass mortalities (Harwood & Hall 1990). Given these limitations, the available data are a highly conservative estimate of the frequency of epidemics in pinniped populations. The mean time-period between the disease outbreaks in harbour seals of northern European waters

is 34.5 years (Table 1). Given a generation time of about 5 years, a disease outbreak will influence at least part of a population every fifth to tenth generation. Diseases thus qualify as 'rare' ecological events in pinniped populations but perhaps only because of our insufficient ability to recognize such events. Alternatively, they may really be rare because the immunological memory of individuals surviving an epidemic makes another outbreak of the same disease in the same population unlikely (Heide-Jorgensen et al. 1992).

Background information on the harbour seal epizootic

The recent harbour seal epizootic was caused by a morbillivirus related to canine distemper virus, but identified as a separate form called phocine distemper virus (PDV; Curran et al. 1990). The disease began in about February to April 1988 in the Kattegat area, spread north along the Norwegian coast and south into the Wadden Sea, until it reached England and Scotland in August to September 1988. The epidemic came to an end in winter and spring 1988–89 when very little further increased mortality was noted (Dietz et al. 1989).

Presumably, the disease was transmitted to harbour seals by harp seals (*Phoca groenlandica*) which, in 1986–88, had invaded in great numbers along the Norwegian coast. The causes of this invasion are largely unknown, but may be related to an oceanographic perturbation in the north Atlantic. A few individuals also reached the Kattegat area. Later investigations showed that, in 1987, 40–50% of the harp seals from the West Ice and Barents Sea populations carried antibodies to PDV (Markussen & Have 1992).

Disease-related mortality

The timing of the major impact of the disease influenced its impact on different age classes in the population. The early infections in April and May of 1988 in the Skagerrak-Kattegat area led to total loss of the 1988 cohort since females either aborted or abandoned their pups. In contrast, in the United Kingdom pup mortality was minor since pups were weaned by the time the disease got to the UK. At that time of year, pups rarely come into contact with other animals because of their reduced tendency to haul out (Thompson & Harwood 1990). In contrast, moulting adults haul out gregariously during that time.

Most animals in the populations were infected even though mortality was quite different among subpopulations. Whereas the Kattegat-Skagerrak, Wadden Sea, Irish Sea and East Anglia populations of harbour seals showed a 40–60% mortality, the Scottish population suffered only a 10–20% mortality (Heide-Jorgensen et al. 1992; Dietz et al. 1989). Of the adult seals

Table 1. Mass deaths of pinnipeds most probably due to biotic factors. The two earliest records about 'harbour seals' may also refer to grey seals. In the case of the walrus the cause of mortality could not be established unequivocally. The so-called 'pox' of the Galapagos seal lion and fur seal clearly is a transmissible disease, but of unknown etiology.

Species	Year	Agent	Effects	Location	Source[a]
Phocids					
Crabeater seal	1955	Virus?	Mass mortality	Antarctica	1
Baikal seal	1987	CDV-like	Mass mortality	Lake Baikal	2, 3
Grey seal	1988/89	PDV	Fewer pups	Britain	4
Harbour seal	ca. 1780	Unknown	Mass mortality	Britain	5
	1813	Unknown	Mass mortality	Orkney	6
	1836	Unknown	Mass mortality	Orkney	6
	1869–1870	Unknown	Mass mortality	Orkney	6
	1918	Unknown	Mass mortality	Iceland	7
	1930	Unknown	Mass mortality	Shetland	8
	1979/80, 82	Avian influenza	Local mortality	New England	9
	1988/89	PDV	Mass mortality	Northern Europe	3, 7
Otariids					
California sea lion	1947	Pneumonia?	Local mortality	California	10
	1968–70	Leptospirosis SMSV?	Abortions, death of subadult males	California	10, 11
South African fur seal	1828	Red tide?	Mass mortality	South Africa	12
Galapagos sea lion	1970–71	('Pox'-virus?)	Mass mortality	Galapagos	13, 14
	1976	('Pox'-virus?)	Mass juvenile mortality	Galapagos	14
	1982–83	('Pox'-virus?)	Mass juvenile mortality	Galapagos	15
Galapagos fur seal	1970–71	('Pox'-virus?)	Small-scale mortality	Galapagos	14
	1976	('Pox'-virus)	Small-scale mortality	Galapagos	14
Odobenid					
Pacific walrus	1978	Unknown	Local mass mort., abortions	Alaska	16

[a]1, Laws & Taylor (1957); 2, Grachev et al. (1989); 3, Heide-Jorgensen et al. (1992); 4, Harwood (1990); 5, Fleming, in Harwood & Hall (1990); 6, McConnell, in Harwood & Hall (1990); 7, Dietz et al. (1989); 8, Bonner (1972); 9, Geraci et al. (1982); 10, Vedros et al. (1971); 11, Smith et al. (1973); 12, Wyatt after Morell, in Harwood & Hall (1990); 13, Rand (1975); 14, Trillmich (1979 and unpubl. obs.); 15, Robinson (1985, and pers. comm.); 16, Fay & Kelly (1980).

in Britain tested in 1989, 88% were seropositive, which indicated almost complete infection of those age-classes, whereas only 12% of tested juveniles were seropositive (Heide-Jorgensen *et al.* 1992). Since this applied also to the Scottish population it suggests that these animals were more resistant to the disease or had lower infective doses, or that the virus had mutated (Thompson *et al.* 1992).

There also appeared to be sex-differences in mortality: in the seal herds infected early 45–60% of the males died (Kattegat), whereas in the herds infected later (UK) 55–75% of the males died (Heide-Jorgensen *et al.* 1992). Perhaps this was due to the fact that males haul out to moult later than females.

The importance of population subdivision

In the Kattegat area the spread of the disease was not density-related, which suggests that social behaviour, in particular gregarious haul-out, always creates local density sufficiently high for disease transmission.

Although the disease spread fast through the harbour seal populations along the coast of the North Sea, some remote populations appeared unaffected. Within the Kattegat and Skagerrak area, the spread between colonies proved to be inversely proportional to distance between herds (Heide-Jorgensen & Härkönen in press). Obviously, migration between haul-out areas is quite frequent as otherwise the disease could not have spread so quickly around the border of the North Sea. However, populations in northern Norway as well as on Iceland and in the Baltic were never affected, which suggests relative isolation from the other populations around the North Sea (but these populations may also have been resistant to the virus).

The grey seal (*Halichoerus grypus*) population showed only limited signs of being affected by the disease. Except for a reduction of 6–24% in pup production in 1988 (Heide-Jorgensen *et al.* 1992) no major effects on grey seal populations were noted. Obviously grey seals were largely resistant to the disease, since seroconversion, i.e. the build-up of antibodies to PDV, occurred in most individuals.

Similarly, the reduced impact of PDV on the Scottish population of harbour seals might indicate that more western populations were less susceptible to the disease. Alternatively, the western stocks may have been less affected because they were hit by the disease in a different stage of their live cycle when contacts between individuals were less frequent and transmission of the disease less likely. It was postulated that seroconversion might have taken place in many cases without clinical signs, perhaps due to low-level infections (Heide-Jorgensen *et al.* 1992).

Conclusions

The effects of the documented rare, catastrophic events on pinniped populations were mainly density-independent. Moreover, the affected populations will take many years to recover from these events. Therefore, rare ecological disasters can keep even pinniped populations well below the estimated carrying capacity of the environment (Harwood & Hall 1990; Reijnders in press).

On the other hand, density-dependent changes of population parameters have been demonstrated for pinnipeds (Fowler 1990) and such effects could reduce the probability of population extinction through environmental catastrophes by increasing the population's growth rate at low densities.

For both abiotically caused reductions in food availability and disease-related mortality, the subdivision of a species into rather isolated sub-populations may be the more important parameter, permitting the species to persist in the face of catastrophic local declines or even local extinctions. Separation of subpopulations and retreat of survivors into optimal habitat reduce the probability of extinction. Sheltered populations, like the sea lions in the Gulf of Cortez during EN, may play a major role in long-term population stability because different stressors will influence each population in a unique way. This would lead to survival of local populations which could then contribute to the repopulation of harder-hit or even extinct populations elsewhere.

The impact of rare events makes migratory behaviour and breeding dispersal very important for long-term population persistence. However, knowledge about dispersal processes is very limited and more information is urgently needed to enable a better assessment of the role of dispersal in long-term population stability in pinnipeds. Distributional shifts during rare events, as exemplified by the emigration of South American fur seals from Peru into Chile, may induce permanent settlement of a new geographical range or of areas where extinction occurred previously.

Lastly, closer attention needs to be given to the investigation of potential biotic causes of population declines because many such events may have been overlooked in free-living populations in the past. To achieve such close documentation and the understanding of population processes deriving from it, long-term monitoring of populations and detailed study of their social behaviour is necessary to evaluate changes in numbers. The variable reaction of harbour seals of different subpopulations to infection with PDV raises the possibility that local populations may be sufficiently different genetically to react differently to parasite challenges. Therefore, dispersal, migration, the role social behaviour plays in the transmission of diseases, and genetic differentiation among populations as well as the role of gene flow need to be studied.

Altogether 'spreading of risk' (den Boer 1968) by the existence of many more or less isolated subpopulations may be as important for populations of large vertebrates as for insect populations. The effects of this spreading, however, will have to be measured on a different time-scale commensurate with the longer lifespan of large vertebrates. Spreading of risk throughout a large geographic range should also be a major aim of conservation strategies to avoid extinction of pinniped species, especially within the perspective of global climate changes.

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