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Mark-recapture and satellite tracking of rehabilitated juvenile grey seals (*Halichoerus grypus*): dispersal and potential effects on wild populations

Cécile Vincent[1,2], Vincent Ridoux[2], Mike A. Fedak[3], and Sami Hassani[1]

[1]*Laboratoire d'Etudes des Mammifères Marins, Océanopolis, BP 411, 29 275 Brest cedex, France*
[3]*NERC Sea Mammal Research Unit, Gatty Marine Laboratory, School of Environmental and Evolutionary Biology, University of St Andrews, Fife KY16 8LB, Scotland, UK*

Abstract

The fate of rehabilitated marine mammals after release is important at both the individual level, concerning the survival and re-adaptation of the animal to the wild environment, and at the population level, regarding the impact of the return of rehabilitated animals for the conservation of local groups. Ninety-two juvenile grey seals (*Halichoerus grypus*), rehabilitated at the Océanopolis Rescue Centre (Brittany, France) from 1989 to 1999, were monitored after release using flipper tags, colour markings, head tags, satellite tags, or photo-identification.

Overall, 48% of the rehabilitated seals were re-sighted after release. Flipper tags, colour markings and head tags allowed recapture of 14%, 35% and 61% of seals fitted with these marks, respectively. When re-sighted alive, the mean number of recapture per seal was 1.0, 1.6 and 2.6, respectively. Flipper tags mostly allowed identification of dead animals. They could remain on the animal for several years, but were difficult to read from a distance. Colour markings and head tags glued to the fur of the seals were more legible and allowed more sightings over a few months. Photo-identification allowed a few individuals to be regularly recaptured over periods of up to 5 years. The use of Satellite Relay Data Loggers brought numerous data about movements at sea, hauling-out, swimming, and diving behaviour of four seals. Despite the short duration of data collection, information was obtained concerning the rapid and long distance dispersal of the seals, as well as their early diving capacities.

Rehabilitated seals showed a rapid ability to disperse over long distances, but also settled in known haul-out sites after only a few months. Consequently, their re-adaptation to the wild seemed successful at the individual level, in terms of social integration and foraging behaviour, whereas, at the population levels, the long-term impact on local grey seal groups remained uncertain, because of the dispersal of many seals soon after release.

Key words: grey seal *Halichoerus grypus*, rehabilitation, tagging, satellite tracking, dispersal, conservation.

Introduction

Public and scientific concerns about live stranded marine mammals have led to the development of rehabilitation facilities. These facilities are included in related institutions (zoos, aquariums) or established for the sole objective of rehabilitation and return to the wild of marine mammals, notably in Northern America and Europe (St. Aubin *et al*., 1996). Despite the increasing number of animals treated in these facilities and released in the wild, few studies have investigated the fate of rehabilitated individuals and their impact on wild populations (Wilkinson & Worthy, 1999). Yet, at least three crucial points should be assessed to monitor the effectiveness of rehabilitation: survival of rehabilitated animals, ability to resume normal life after release, and contribution of rehabilitation programs to the conservation of wild populations. In the USA, the National Marine Fisheries Service (NMFS) has required that released animals be marked or tagged so that they can be identified if the strand again (Wilkinson & Worthy, 1999). In European countries, such global recommendations do not exist, and establishment of monitoring programs for rehabilitated marine mammals relies on local policies or initiatives.

[2]Current address: Laboratoire de Biologie et Environnement Marins, E.A. 3168, Université de La Rochelle, Avenue M. Crépeau, 17000 L Rochelle, France.

To date, most techniques used for monitoring movements and behaviour or rehabilitated marine mammals consisted of either visual marks (Seagars, 1988; Ridoux *et al*., 1998), or telemetry tools, such as satellite and VHF transmitters (Gales & Waples, 1993; Mate *et al*., 1994; Westgate *et al*., 1998; Lander *et al*., 2000) attached to the animals. While the first allows opportunistic observations over periods of varying length (depending on the attachment system), telemetry allows continuous or frequent tracking and behavioural data recording for short period after release (from days to weeks, possibly months).

In the present study, we describe the results obtained from the use of these different techniques, as well as photo-identification, applied on rehabilitated grey seals (*Halichoerus grypus*) in France over the last decade.

Grey seals are at the southern limit of their breeding range in France, where residents haul-out groups are estimated at only 100–150 individuals, with an annual pup production of about 5 pups/year (Vincent, 2001). The size and status of the local grey seal group were assessed only recently. In the early 1980s, when rehabilitation facilities were established in France, the species was classified as 'vulnerable' and management plans incited both rehabilitation of live stranded seals and establishment of marine protected areas. The seals movements between the French and the British colonies were not documented, and long-term maintenance of French groups were thought to rely largely on local production. In addition, tens of yearlings are found dead or alive along the west coast of France each year. During the past decade, an average of 15 juvenile grey seals were found dead stranded each winter, together with 13 others live strandings (Creton *et al*., 1996). From 1989 to 1999, 133 individual seals were admitted at the Océanopolis Rescue Centre, of which 92 were rehabilitated and released at sea. The fate of these young seals was regarded as a crucial issue for the maintenance of the local population, due to low pup production, high by-catch, and natural mortality rates of juvenile grey seals. Dispersal and behaviour of the rehabilitated seals therefore constituted a key issue in evaluating the role of the rescue centre as a conservation strategy for the grey seal in France.

The objectives of the study were to: (1) describe the recapture rates and dispersal of rehabilitated seals after release, by using different mark-recapture techniques and telemetry, (2) determine how individual seals released in their natural environment behave after several months of human care by using satellite tags, and (3) evaluate the long-term effect of rehabilitated juveniles on the maintenance of the local grey seal haul-out groups.

Materials and Methods

Rehabilitated seals

From 1989 to 1999, 92 grey seals were taken in the Océanopolis Rescue Centre and released at sea. They were young of the year, aged between a few days and a few months, as assessed from the presence of white coat for un-weaned pups or body weight for weaned seals. Most seals stranded in Brittany, France, but some stranded as far south as Spain. Stranded seals were generally admitted between December and February and released from March to June. The basic reason for their stranding was severe malnutrition, because their average body mass at stranding was about 17 kg (14.8 kg for neonates), which is less than half of the average body mass at weaning (Fedak & Anderson, 1982).

From 1989–90, rehabilitation was purposefully kept to a minimum duration (one month maximum) to minimise human imprinting. However, it soon appeared that the success of this strategy was poor as indicated by a large proportion of animals stranding again soon after their release as a consequence of insufficient fat reserve. From 1991 on, the seals were kept in captivity until their body mass reached 40–45 kg, the average body mass at weaning (Fedak & Anderson, 1982). The rarity of re-admission of rehabilitated seals from 1991 onwards may indicate the previous lighter seals were not ready for release.

Mark-recapture techniques

Flipper tags—All rehabilitated seals were identified with Jumbo Rototags (Dalton Supplies Ltd., Henley-on-Thames, Oxfordshire, UK). The self-piercing tags were applied to the inter-digital web of the hind flipper using specially designed pliers. These orange cattle ear tags bear a series number on one limb and mention the London Zoo on the other one for the return of information (Summers & Whitthames, 1978; Erickson *et al*., 1993). These tags are supposed to be permanent markings, but are known to be lost at an increasing rate with age (Stobo & Horne, 1994; Pistorius, *et al*., 2000).

Colour markings—From 1989 to 1997, a combination of two colours or numbered head markings were glued on the fur of the seal with epoxy resin (Araldite). Two flat plastic plates, forming a colour code and slightly bent to accommodate the top of the head's shape, were used (Fig. 1).

Head tags—Similarly, numbered head tags (Hall *et al*., 2000) were used from 1997 onwards. These pyramidal markings, about 4 cm high and 6 cm in diameter at the base, also were glued on the top of the head of the seals with quick-setting epoxy resin. They were provided by the Sea Mammal

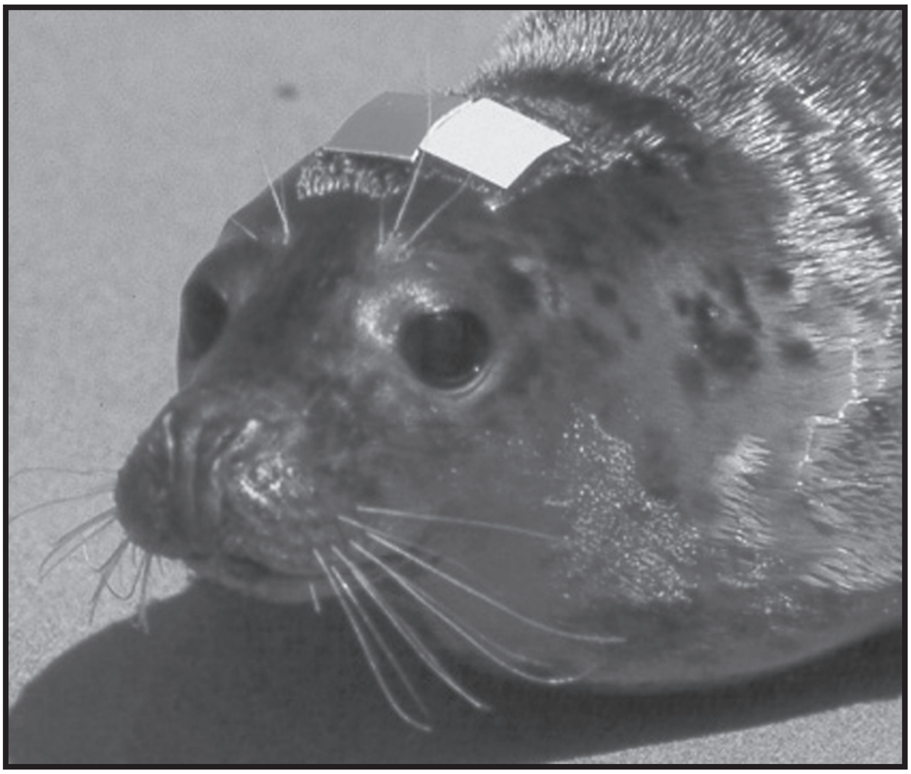

Figure 1. Combination of two colour plastic markings ('colour markings' in the text) on the fur of the grey seal with quick setting epoxy resin.

Research Unit (SMRU, UK), and a phone number was printed on the marking in addition to the identification number of the seal.

Natural markings—The pelage of grey seals displays natural markings, typically black spots over a light background, that can be used for photo-identification (Hewer & Backhouse, 1959). From 1995 onwards, the rehabilitated seals were photo-identified prior to their release and their photos matched with those taken in the main grey seal haul-out sites in France between April 1998 and August 2000 (Vincent, 2001). Twenty-three males and 20 females were photographed before release from 1995 to 1999. However, only 9 males and 16 females were considered suitable for photo-identification, as assessed from the legibility of their natural pelage pattern (Vincent *et al*., 2001).

Satellite tags—In May 1997, four female grey seals were tagged with Satellite Relay Data Loggers (SRDL; SMRU, Fig. 2), allowing transmission of behavioural data (diving, swimming, and time spent ashore), as well as location of the seal at sea or on land via the ARGOS Location System (Fedak *et al*., 1996; Service Argos, 1996). Haul-out periods were recorded, as well as dive durations and maximum dive depths. Detailed behavioural data will be presented elsewhere, so that only a summary of maximum dive depths reached by the seals are presented here. The tags were glued to the nape of the seals, using quick-setting epoxy resin. Four female grey seals were fitted with satellite tags; two seals (#22482 and #22487) were taken in as unweaned pups, whereas the two others (#22485 and #22486) were a little older on arrival. Seal #22482 and #22485 were released on 2 June 1997, and the others on 13 June 1997. They were all released at the western point of Brittany, close to the grey seal group of the Molène Archipelago (Brittany, France).

Results

Recapture rates

Marking techniques allowed opportunistic observation of rehabilitated seals, either dead or alive, mostly on shore, but also at sea (notably some observations from fishermen or divers; Table 1).

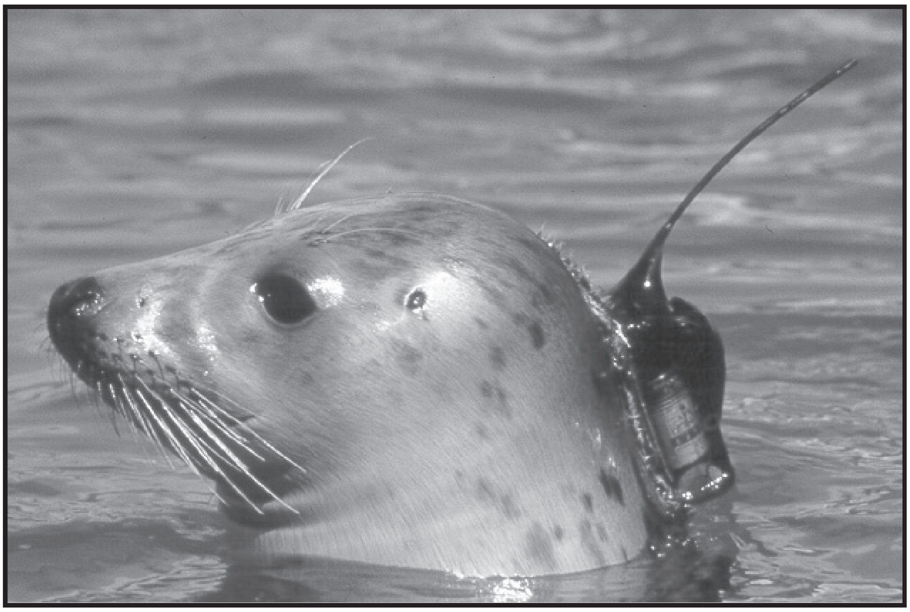

Figure 2. Satellite relay data logger (SMRU, UK) glued to the nape of a grey seal with quick setting epoxy resin. The tag is placed high enough to emerge as often as possible when the seal is at the surface, in order to allow transmissions, without the antenna appearing in the field of vision of the animal.

Table 1. Number of grey seals, dead or alive, re-sighted and identified thanks to their markings after release at sea. Even if many seals were released with more than one mark, these figures only take into account the mark or tag that effectively allowed primary identification of the seal in the field (no double count in columns 2 and 3).

	Number of seals released with markings	Number of seals re-sighted dead	Number of seals re-sighted alive	Total number of sightings of living seals
Flipper tags	92	7	6	6
Colour markings	40	6	8	13
Head tags	28	6	11	29

Overall, 48% of the 92 rehabilitated seals were re-sighted after release. Flipper tags, colour markings, and head tags allowed recapture of 14%, 35% and 61% of seals fitted with these marks, respectively. When re-sighted alive, the mean number of recapture per seal was 1.0, 1.6 and 2.6, respectively.

Among the 25 rehabilitated seals photo-identified, only two males and one female were re-sighted in the field. They were re-sighted 49, 4 and 16 times, for periods reaching 5 years, 2 months and 3 years after release, respectively.

Satellite tracking allowed continuous recording of movements and behaviour of the seals during 37, 14, 18 and 80 days for seals #22482, #22485, #22486 and #22487, respectively. The average number of locations per day was 6, 5, 5 and 4, respectively.

Dispersal

Flipper tags, colour markings and head tags—Figure 3 shows the location of re-sightings of rehabilitated seals along the coasts of Brittany or further off the release point. Some seals dispersed along the coasts, but observations were often made close to one of the two grey seal haul-out sites in France, the Molène Archipelago and the Sept-Iles Archipelago. This was particularly true for observations reported more than 6 months after release. Eight re-sightings were reported from across the English Channel, with one seal in Ireland, two in the Channel Islands and five in Cornwall, England. Three tags also were found alone on the beaches; a flipper tag in Devon, Southwest England, a head tap in Jersey, and another one in Wales. They were all found more than 6 months after release; however, they could

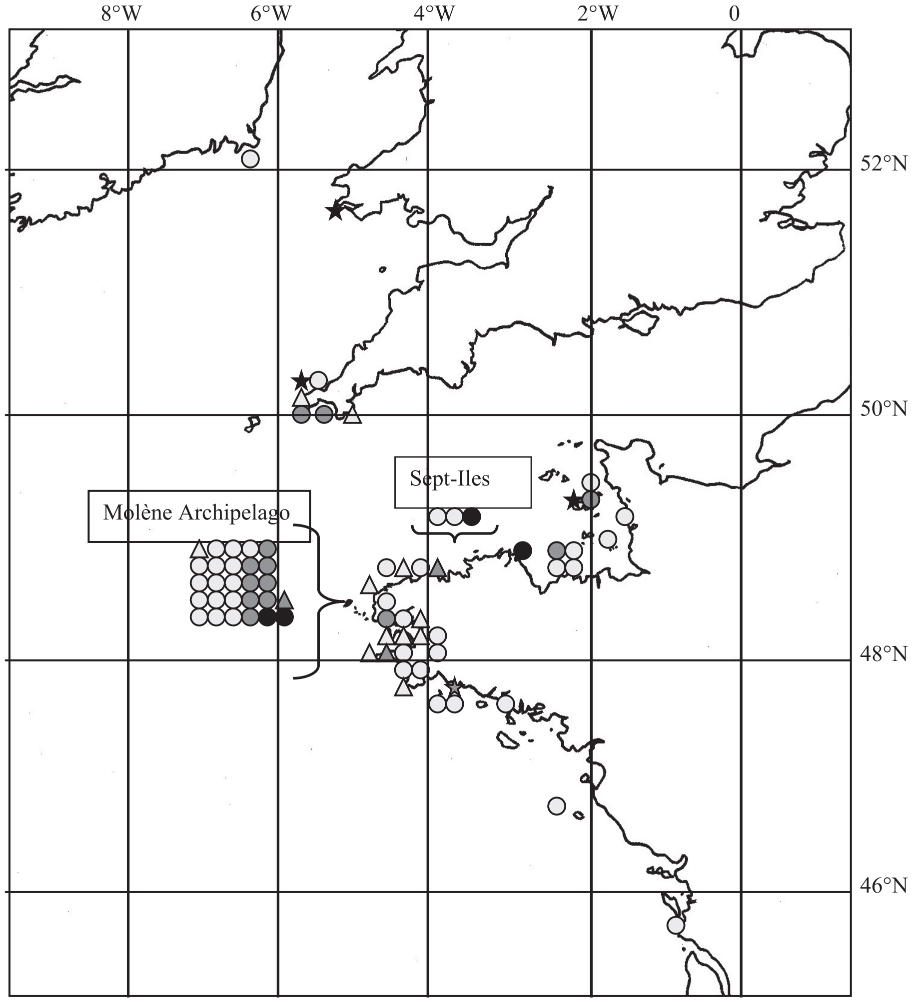

Figure 3. Distribution of re-sightings of marked grey seals after release. The two major grey seal haul-out groups of the Molène archipelago (Mo) and the Sept-Iles archipelago (Se) are indicated. Observations of living (circles) or dead seals (triangles) are reported, as well as return of markings alone (stars). Depending on the delay between the release of the rehabilitated seal and the observation in the wild, the marks are in light grey (<2 months), dark grey (between 2 and 6 months) or black (>6 months).

detach from the animals sooner and wash-up elsewhere.

Satellite tags—Seal #22482—traveled directly northwards, reaching Cape Cornwall after 3 days and continuing to South-east Ireland (Fig. 4). During this 8-day trip, she first made shallow dives (20–25 m), far from the sea bed of the English Channel. Between Wales and Ireland, she began to reach the bottom, at about 120 m deep. She remained at the haul-out site of the Great Saltee (Southeast Ireland) for a couple of days, and then continued her trip northwards. Along the East coast of Ireland, she switched between coastal activity, around known grey seal haul-out sites, and trips at sea in the deep Irish Sea. Her deepest dives reached 169 m. She finally settled near Dunany Point for 3 weeks, and the tag transmissions ended on 9 July, probably short of power.

Seal #22485—moved immediately along the Breton coast, diving to the bottom from the first day and sometimes reaching 120 m, the maximum depth available in the area. On 8 June, she passed the grey seal group of the Sept-Iles Archipelago, and crossed the Channel within 2–3 days. During this trip, she dove to the bottom at about 90 m. She

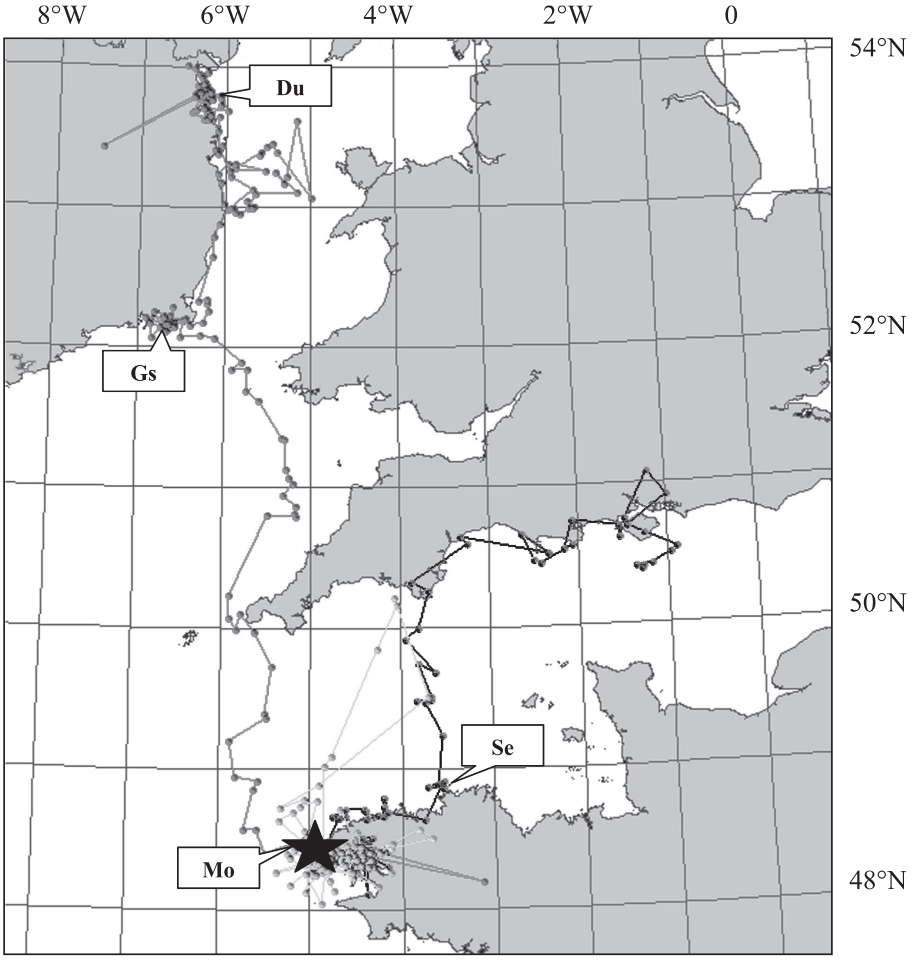

Figure 4. Map of satellite tracking of four female rehabilitated grey seals. The grey seal haul-out sites visited by the seals are indicated as follows: Mo = Molène archipelago, Se = Sept-Iles archipelago, Gs = Great Saltee, and Du = Dunany Point. The track of seal #22482 is shown in dark grey, seal #22485 in light grey, and seal #22487 in black. Seal #22486 stayed within the Molène archipelago during the whole track, so that it is hidden under other location plots in the area. A black star indicates the point of release of all seals.

continued her trip eastwards along the South coast of England, from Dartmouth to the Isle of Wight. Signals ended abruptly on 15 June, before the expected power shortage.

Seal #22486—immediately settled in the Molène Archipelago. She rarely traveled outside the area, making shallow dives (10–20 m) in the vicinity of known haul-out sites. Transmissions ended prematurely on 1 July, and the female was found dead in the area on 24 July. The severe decomposition of the carcass did not allow determination of the cause of death.

Seal #22487—first behaved as seal #22486. She hauled-out regularly in the Molène Archipelago, and only dived in shallow waters (dive and sea-bed depths at −10 or −20 m) around the haul-out sites. However, she made several trips outside the archipelago, diving progressively deeper; on 28 July, she crossed the Channel and reached the Bay of Plymouth within 3 days. She barely stayed there and travelled back across the Channel, she dived as deep as 100 m to 130 m. She returned to the Molène Archipelago and hauled-out there until the end of transmissions on 5 September, the tag running out of batteries; however, during this last month she regularly dived deeper than at the beginning of the track (40 to 70 m). This female was observed a few months after the end of transmissions on the coast of Brittany, in good health.

Photo-identification—one male was stranded and rescued in January 1995 and released in April 1995 with colour markings. This male was not re-sighted for 3 years, but was photo-identified regularly between April 1998 and August 2000 in the Molène Archipelago. It was visually recaptured during most seasons (the annual moult, the post-moult and summer seasons and the breeding season), with a total of 49 re-sightings. Another male, released in June 1998, was photo-identified four times in the Molène Archpelago during the two following months, and was not re-sighted after. Lastly, one photo-identified female, also fitted with satellite tag #22487, was re-sighted 16 times in the Molène Archipelago, between May and July 1998, 1999 and 2000, with the exception of one observation in October 1999.

Discussion

Comparative use of mark-recapture techniques and satellite tracking

'Traditional' marks, such as flipper tags, colour markings, or head tags, are very cheap and can be deployed on virtually all rehabilitated animals.

Flipper tags are permanent markings allowing identification of an animal several years after release, as confirmed by the observation of adult rehabilitated seals fitted with these tags. However, a significant loss rate has been described by several authors (Stobo & Horne, 1994; Pistorius *et al*., 2000). Additionally, the identification number of the tags are difficult to read from a distance on living seals in the wild, making this tag more effective in identifying seals found dead or alive stranded in bad condition.

By contrast, colour markings and head tags were more legible from a distance (cf. Table 1). Observers were more successful in re-sighting and identifying seals with head tags, probably due to their height over the heads of the seals. However, in contrast to the flipper tags, they both last a few months after release and were shed with the moult.

Photo-identification of individual natural pelage markings was the least intrusive technique for identifying seals, and appeared to be of great interest over the long term. Two seals were regularly re-sighted several years after their release, constituting the longest and most complete series of individual recaptures. Inclusion of photo-ID pictures of rescued animals in larger catalogues (e.g., Hiby, 1994) potentially can provide recaptures of released animals far away from the release site using an automated matching software (Hiby & Lovell, 1990). One limitation of this technique is the unsuitability of certain categories of seals such as males (sometimes evenly black), and the changes in pelage pattern during the first year of life of the seals (Vincent *et al*., 2001).

A major characteristic of all techniques described above is the opportunistic nature of individual re-sightings. The identification and report of a marked seal rely on presence of observers, publicity of the releasing program for return of information, and establishment of a photo-identification program in the wild grey seal populations. The higher rate of recapture for seals released during the last years of the study could be partly attributed to better publicity acquired by Océanopolis at both the local and international scale for return of information. Additionally, the greater concentration of recapture in the Molène area and the Sept-Iles area may be a combination of the rehabilitated seals being attracted by the resident seal groups or to the higher observation effort in these areas.

Satellite tracking, by contrast, allows frequent remote location of an animal. The attachment system results in the loss of the tag when the fur of the seal is shed during the annual moult; however, many tags stop emitting before they detach due to shortage of batteries. In the present study, the duration of the satellite tracking was shortened by a preliminary experiment conducted in captivity during 2 to 4 weeks, for assessing the accuracy of ARGOS locations (Vincent *et al*., 2002).

The combination of different identification or tracking techniques is possible, and even encouraged for a better probability of re-sighting of seals over time. A particular technique might also be chosen from financial aspects, satellite telemetry being by far the most expensive, while other techniques are cheap. All tags seemed to be well supported by the seals, as determined by visual observation of the seals before release; however, detailed studies would be necessary to further document this aspect. Holes or splits in the inter-digital web of the hind flippers of seals were reported, as already described by Stobo & Horne (1994). Some authors also reported skin damage in grey seals due to the use of glue; however, in our study the seals photo-identified after their moult had a normal pelage, with no damage visible where the tag was glued.

Dispersal of rehabilitated seals

Two major results were drawn by the tracking of rehabilitated seals, released at sea after several months of human care: they have a great ability of long distance dispersal, and tend to haul-out in known grey seal colonies.

Satellite tracking was by far the most efficient tool to investigate distant movements (Fig. 4), with inexperienced seals travelling over hundreds of km within days. Long distance dispersal of juveniles has already been described in free ranging grey seals

(Bonner & Whitthames, 1974; Bonner, 1981; Prieur & Duguy, 1981). Our results from satellite tracking therefore confirm that rehabilitated seals keep this ability to disperse widely in their first year. Other tagging techniques also documented movements of rehabilitated seals between Brittany and Wales, Ireland, Southwest England and the Channel Islands (Fig. 3). We assumed that the proportion of re-sightings reported in foreign countries would have been higher if recapture probabilities would have been equal, given the influence of local publicity of seals rehabilitation (for visual mark-recapture).

Observations made in France showed individual dispersion scattered along the coasts of Brittany in the first weeks or months following release, and re-sightings were rather grouped around known grey seal haul-out sites after longer periods (Fig. 3). These figures suggest that, after a first period of exploratory dispersal, rehabilitated seals haul-out within known grey seal groups. One can argue that these known haul-out sites were monitored more frequently, which certainly accounted for the high proportion of re-sightings. The same explanation can be suggested for individuals being recaptured in grey seal colonies in the British Isles. However, satellite tracking provided an independent estimate of haul-out site use by the rehabilitated seals, the four females hauling-out only in known grey seal groups.

Re-adaptation to the wild

Survival in the wild of released animals is the first parameter to examine in assessing the success of rehabilitation (Wilkinson & Worthy, 1999). Of all seals released, 20.7% were found dead, which represents 43.2% of the seals for which recapture data are available. None of these figures can be considered as mortality rates because a number of carcasses can stay unreported. Still, we can state that mortality rate is at least 20.1%, and possibly 43.2%. These figures are well within the estimated 40–80% wild grey seals that die within their first year of life (Hall *et al*., 2001).

Another aspect of the success of the rehabilitation of juvenile seals is their behaviour after release. Two important behaviours can be distinguished; foraging behaviour, by which the seal will be able to eat again by itself, and social behaviour, ultimately necessary for reproduction several years after.

The four seals fitted with satellite tags showed a rapid development of diving ability, which typically infers foraging behaviour. The most striking example was seal #22482, taken in before weaning (she learned how to swim, dive to shallow depths, and eat solid food during rehabilitation), who dove as deep as 169 m only 3 weeks after release. The other seals fitted with satellite tags did not dive as deeply because they remained in shallower waters, but also rapidly reached the sea bed. It is not possible to say whether these dives were successful in terms of prey capture, but the diving behaviour of these young rehabilitated seals was similar to that of older free-ranging seals foraging on benthic prey (e.g., McConnell *et al*., 1992; 1999). Also, seals visually re-sighted months or years after their tracking were in good condition, indicating that they were successfully capable of foraging.

The other aspect was the rapid integration of rehabilitated seals in wild grey seal groups. In addition to their frequent use of known haul-out sites, most seals visually observed in haul-out groups were mixed with other wild seals.

Potential impact on local grey seal groups

The impact of rehabilitation of malnourished or injured juvenile seals on the maintenance or conservation of local grey seal groups remains difficult to assess. The rapid movements of rehabilitated seals after release, sometimes over several hundreds of kilometres within a few weeks, can be opposed to the significant proportion of re-sightings in particular in the two French haul-out sites. If the integration of rehabilitated seals in wild groups seems effective, the local groups or sub-populations to which these seals will finally belong is difficult to assess. In particular, recent studies have shown that grey seal groups in France probably consist of individuals occurring seasonally on different haul-out sites in France and in the British Isles, rather than constituting sedentary groups (Vincent, 2001). If rehabilitated seals follow the patterns of movements of wild seals, such long-distance movements may persist over their life time.

Several authors argue that a population would only benefit from the rehabilitation of a given animal if this individual reaches sexual maturity and reproduces (LeBoeuf, 1996). We were not able to investigate the reproductive performance of surviving rehabilitated seals. Assessing such a parameter implies long-term monitoring of rehabilitated seals, which proved to be extremely difficult. Additionally, recent studies have shown that female grey seals tend to be very faithful to their breeding site, and particularly reproduce on the site where they were born (Pomeroy *et al*., 2001). This brings an important question about the origin of rehabilitated seals. While the few rehabilitated pups (wearing their typical white coat) were most probably born in Brittany, previous tagging data have shown that yearlings found on the French coasts sometimes originated from distant breeding sites (Prieur & Duguy, 1981; Siorat *et al*., 1993). Therefore, the site of birth of the majority of rehabilitated seals remains unknown. Genetic studies including samples from close haul-out groups would be necessary to describe the genetic structure of grey seal sub-populations in the Southwest British Isles, and therefore better investigate the impact of rehabilitation activities on local grey seal groups.

While reintroduction of rehabilitated animals into wild populations regularly provokes controversial discussions (St. Aubin *et al*., 1996; Wilkinson & Worthy, 1999), far beyond the subject of this study, the fate of these rehabilitated animals after release does not often constitute a priority field of investigation. However, we consider it as a key issue in the evaluation of the role of rehabilitation centres, both at the individual and population level. We could observe the individual success of reintroduction of rehabilitated juvenile grey seals to the wild. However, the impact of rehabilitated seals on wild populations remained unclear at the local scale. This uncertainty could be linked to the status of grey seals in France, as free-ranging seals seem to move between different French and British haul-out sites (Vincent, 2001). These recent data highlight the need for combined studies of free-ranging and rehabilitated animals, especially when local concerns on the conservation of the species did encourage the establishment of rehabilitation facilities.

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Literature Cited

Bonner, W. N. & Witthames, S. R. (1974) Dispersal of common seals (*Phoca vitulina*), tagged in the Wash, East Anglia. *Journal of Zoology, London* **174,** 528–531.

Bonner, W. N. (1981). Grey seal, *Halichoerus grypus*. In: Ridgway, S. H. & Harrison, R. J. (eds.) *Handbook of marine mammals*. Academic Press, London.

Creton, P., Menegaz, J. M., Menguy, A., Collet, A. & Ridoux, V. (1996) Echouages et soins aux phoques en Bretagne: 1973–1994. *Mammiferes marins en Bretagne, Penn ar Bed* 23–32.

Erickson, A. W., Beste, M. N. & Laws, R. M. (1993) Marking techniques. In: R. M. Laws (ed.). *Antarctic Seals: Research Methods and Techniques*, pp. 89–118. Cambridge University Press, Cambridge.

Fedak, M. A. & Anderson, S. A. (1982) The energetics of lactation: accurate measurements from a large wild animal, the grey seal (*Halichoerus grypus*). *Journal of Zoology, London* **198,** 473–479.

Fedak, M. A., Lovell, P. & McConnell, B. J. (1996) MAMVIS: A marine mammal behaviour visualization system. *Journal of Visualization and Computer Animation* **7,** 141–147.

Gales, N. & Waples, K. (1993) The rehabilitation and release of bottlenose dolphins from Atlantis Marine Park, Western Australia. *Aquatic Mammals* **19,** 49–59.

Hall, A., Moss, S. & McConnell, B. J. (2000) A new tag for identifying seals. *Marine Mammal Science* **16,** 254–257.

Hall, A. J., McConnell, B. J. & Baker, R. J. (2001) Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Applied Ecology* **70,** 138–149.

Hewer, H. R. & Backhouse, K. M. (1959) Field identification of bulls and cows of the grey seal, *Halichoerus grypus*. *Proceedings of the Zoological Society of London* **132,** 641–649.

Hiby, A. R. (1994) Abundance estimates for grey seals in summer based on photo-identification data. In: Hammond, P. S. & Fedak, M. A., (eds.) *Final Report to the Ministry of Agriculture, Fisheries and Food under Contract MF0503*. Pp. 5–22. Sea Mammal Research Unit, Saint-Andrews, UK.

Hiby, A. R. & Lovell, P. (1990) Computer aided matching of natural markings: a prototype system for grey seals. *Report of the International Whaling Commission.* Special **12,** 57–61.

Kiely, O., Lidgard, D., McKibben, M., Connolly, N. & Baines, M. (2000). Grey seals: Status and monitoring in the Irish and Celtic seas. Interreg Report, Cork, 76 pp.

King, J. E. (1983) *Seals of the World*. Oxford University Press, Oxford, England.

Lander, M. E., Gulland, F. M. D. & DeLong, R. L. (2000) Satellite tracking a rehabilitated Guadalupe fur seal (*Arctocephalus townsendi*). *Aquatic Mammals* **26,** 137–142.

LeBoeuf, B. J. (1996) Behavioral issues in returning marine mammals to their habitat. In: *Rescue, Rehabilitation, and Release of Marine Mammals: an Analysis of Current Views and Practices*. Proceedings of a workshop held in Del Plaines, Illinois, 3–5 December 1991.

U.S. Department of Commerce, NOAA Technical Memorandum NMFS-OPR-8.

McConnell, B. J., Chambers, C., Nicholas, K. S. & Fedak, M. A. (1992) Satellite tracking of grey seals (*Halichoerus grypus*). *Journal of Zoology, London* **226,** 271–282.

McConnell, B. J., Fedak, M. A., Lovell, P. & Hammond, P. S. (1999) Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology* **36,** 573–590.

Mate, B. R., Stafford, K. M., Nawojchik, R. & Dunn, J. L. (1994) Movements and dive behavior of a satellite-monitored Atlantic white-sided dolphin (*Lagenorhynchus acutus*) in the Gulf of Maine. *Marine Mammal Science* **10,** 116–121.

Pistorius, P. A., Bester, M. N., Kirkman, S. P. & Boveng, P. L. (2000) Evaluation of age- and sex-dependent rates of tag loss in southern elephant seals. *Journal of Wildlife Management* **64,** 373–380.

Pomeroy, P. P., Worthington Wilmer, J., Amos, W. & Twiss, S. D. (2001) Reproductive performance links to fine scale spatial patterns of female grey seal relatedness. *Proceedings of the Royal Society B.* **268,** 711–717.

Prieur, D. & Duguy, R. (1981) Les phoques des côtes de France: III Le phoque gris (*Halichoerus grypus*). *Mammalia* **45,** 83–98.

Ridoux, V., Hall, A. J., Steingrimsson, G. & Olafsson, G. (1998) An inadvertent homing experiment with a young ringed seal, *Phoca hispida*. *Marine Mammal Science* **14,** 883–888.

Seagars, D. (1988) The fate of released rehabilitated pinnipeds based on tag-resight information: a preliminary assessment. National Marine Fisheries Service, Southwest Region Administrative Report SWR-86-5. 34 pp.

Service Argos. (1996) *User's Manual*. CLS Argos. 184 pp.

Siorat, F., Duguy, R. & Ridoux, V. (1993) Histoire d'une population de phoques gris aux Sept-Iles. *Penn ar Bed* **150,** 32–37.

St. Aubin, D. J., Geraci, J. R. & Lounsbury, V. J. (1996) Workshop summary and recommendations. In: *Rescue, Rehabilitation, and Release of Marine Mammals: an Analysis of Current Views and Practices*. Proceedings of a workshop held in Del Plaines, Illinois, 3–5 December 1991. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-OPR-8.

Stobo, W. T. & Horne, J. K. (1994) Tag loss in grey seals (*Halichoerus grypus*) and potential effects on population estimates. *Canadian Journal of Zoology* **72,** 555–561.

Summers, C. F. & Whitthames, S. R. (1978) The value of tagging as a marking technique for seals. In: Stonehouse, B., (ed.) *Animal Marking: recognition marking of animals on research*, pp. 63–70. McMillan.

Vincent, C. (2001) Ecological bases for the conservation of the grey seal *Halichoerus grypus* in the Iroise Sea, France. PhD Thesis, University of Brest, France. 220 pp.

Vincent, C., Meynier, L. & Ridoux, V. (2001) Photo-identification in grey seals: legibility and stability in natural markings. *Mammalia* **65,** 636–372.

Vincent, C., McConnell, B. J., Fedak, M. A. & Ridoux, V. (2002) Assessment of Argos location accuracy from satellite tags deployed on captive grey seals. *Marine Mammal Science* **18,** 156–166.

Westgate, A. J., Read, A. J., Cox, T. M., Schofield, T. D., Whitaker, B, R. & Anderson, K. E. (1998) Monitoring a rehabilitated harbor porpoise using satellite telemetry. *Marine Mammal Science* **14,** 599–604.

Wilkinson, D. & Worthy, G. A. J. (1999) Marine mammal stranding networks. In: Twiss, J. R. & Reeves, R. R. (eds.) *Conservation and Management of Marine Mammals*. pp. 396–411. Smithsonian Institution Press, Washington.