NOT TO BE CITED WITHOUT PRIOR
REFERENCE TO THE AUTHOR(S)

Northwest Atlantic Fisheries Organization

Serial No. N2608 NAFO SCR Doc. 95/86

SCIENTIFIC COUNCIL MEETING - SEPTEMBER 1995
Symposium - The Role of Marine Mammals in the Ecosystem

Anisakid (Nematoda) Infections in Icelandic Grey Seals (*Halichoerus grypus* Fabr.)

by

D. Ólafsdóttir[1] and E. Hauksson[2]

[1] Marine Research Institute, Skulagata 4, P. O. Box 1390,
121 Reykjavik, Iceland

[2] Icelandic Fisheries Laboratories, Skúlagata 4, P. O. Box 1405
121 Reykjavik, Iceland

Introduction.

Four species of Anisakidae nematodes are frequently observed in seal-stomachs in the North-Atlantic. They are Pseudoterranova decipiens, Contracaecum osculatum, Phocascaris cystophorae and Anisakis simplex (1). The life cycles of these species are similar and were summarized by Olafsdottir and Hauksson(2).

Investigations on nematodes in Icelandic seals have previously been performed by Pálsson in 1977 (3) and Olafsdottir and Hauksson, working with samples collected in 1979-83 (2). The present paper adds further information on seasonal and regional variations in nematode-infections in grey-seals Another purpose of the study was to estimate a possible change in the nematode-burden in the main final-host of P. decipiens in Icelandic waters, in the last decade.

Methods.

The samples were collected from the local seal-hunters in the years 1989-93. Most samples were collected from Breidafjord, Faxafloi and the South-Coast but fewer from other areas with scarcer distribution of grey-seal, especially the North- and the East-Coasts (Fig 1). The samples from Breidafjord and Faxafloi were obtained from May to the end of November but the samples from the South-Coast were mostly collected in the period from September to November. Samples from December to April were few in all areas (see Table 2).

Worms in the oesophagus were pressed into the stomachs before the latter was cut from the rest of the digestive tract. The lower jaw and the sex-organs were removed for age and sexual stage analyses. The age of the seals was found by counting growth-layers in their teeth (4). Each age-class of males and females was given weight-values deriving from previous studies on grey seals (4). The mean weights values of the seals behind the data are shown in table 1.

The worms were separated from the stomach-contents and picked from the stomach-wall. They were stored in 70% isopropanol and clarified in 90% lactic acid for identification. Subsamples of at least 200 worms were taken from large samples. The sex of mature worms was identified in all cases but A. simplex and no attempt was made to distinguish between small Contracaecum sp. and Phocascaris sp. larvae.

Statistical comparisons were made on the total number of worms, the number of P. decipiens and C. osculatum as well as the proportions of mature worms of these same species, from seals from Breidafjord, Faxafloi and the South-Coast.

The number of P. decipiens and C. osculatum in seal-stomachs from Breidafjord was also compared with data from a previous study on samples collected in 1979-82.

The comparisons of infections between areas, males and females and between investigations from 1979-82 and 1989-93 were made using analyses of covariance (ANCOVA) with the seal's weight and the months of the year as covariates. The level of significance was tested by paired comparisons by using the Tukey-Kramer method (5).

All worm-counts (x) were transformed with Ln(x+1) and the proportions of mature worms were transformed with arcsin$(x)^{0.5}$ before statistical calculations. The level of significance was in all cases set to 5%.

Results.

Anisakids in grey-seal stomachs.

The four intestinal anisakid-species which survive in seals were all found, in all areas and seasons, in the grey-seal-

stomachs (Table 2). The most common species were P. decipiens and C. osculatum. P. cystophorae occurred sporadically and in small abundances in the stomachs. A. simplex-worms were also rare. They were occasionally found at a premature stage and only in one occasion was a fully mature female observed. The largest and best developed A. simplex worms were found in seals from the South-Coast in the autumn and in stomachs with low infections. Hysterothylacium aduncum was found in few seal-stomachs in addition to the four main-species.

Crater-like wounds were frequently observed in the seal-stomachs. Small larvae, probably Contracaecum sp./ Phocascaris sp. and larger worms, probably C osculatum, were often found stuck to the stomach wall in clusters around the craters.

The seal-stomachs investigated, did all host some anisakids. The youngest pups in the catch were from January off the North-Coast and the total numbers of worms were already 139 to 382 (Table 2e). The anisakid-infections in the pups seem to grow fast in the first months of the seal's life and soon reach the levels of the older seals. The species-composition of worms in pups is also similar to the compositions in older seals (Table 2).

Comparisons of anisakid-infections between sexes, months and areas.

The difference of anisakid-infections in males and females is not significant but it covariates significantly with the weight of the seals ($F_{1,171}$=8,37; p=0,004; slope=0,01). Comparisons of P. decipiens and C. osculatum give the same results. No significant difference is observed between the sexes (fig 3,4,5 and 6,7,8) but the number of worms covariate with the seal-weight (P. decipiens: $F_{1,171}$=9,53; p<0,001; slope=0,01;, C. osculatum: $F_{1,171}$=10,60; p=0,001; slope=0,01).

Changes in the total number of worms by months in grey-seals from Breidafjord, Faxafloi and the South-Coast are not significant (fig. 2). The abundance of P. decipiens, on the other hand, increases significantly ($F_{1,171}$=21,13; p<0.001, slope=0.21) (fig. 3,4,5) and the abundance of C. osculatum

decreases ($F_{1,171}$=12,82; p<0.001; slope=-0.174) (fig 6,7,8) from spring to autumn.

Comparisons on nematode-infections between areas indicate a significant difference on the total number of worms ($F_{2,171}$=13,51; p<0.001). The total abundance of worms is highest in Breidafjord and lowest in seals from the South-Coast. Comparison of pares indicates that the significance originates only from the difference between these two areas ($|Y_1-Y_2|$=0.71; $MSD_{0.01[3.176]}$=0.49).

Comparisons of the abundance of P. decipiens between areas is also significant ($F_{2,171}$=22.86; p<0.001). It is highest in seals from Faxafloi but lowest in seals from the South-Coast (fig. 3,4,5). Comparisons of pares give no significance between Faxafloi and Breidafjord but a significant difference in P. decipiens infections in seals from the South-Coast and Faxafloi ($|Y_1-Y_2|$=1,09; $MSD_{0.01[3.176]}$=0.82) and also in seals from the South-Coast and Breidafjord ($|Y_1-Y_2|$=0,96; $MSD_{0.01[3.176]}$=0.71).

Comparisons of the abundance of C. osculatum between areas is significant ($F_{2,171}$=19.17; p<0.001). The infections are largest in seals from Breidafjord but smallest in seals from Faxafloi (fig. 6,7,8,). Comparisons of pares indicate a significant difference between all three areas. The difference is largest between Breidafjord and Faxafloi ($|Y_1-Y_2|$=1.49; $MSD_{0.01[3.176]}$=0.80) but smaller between Breidafjord and the South-Coast ($|Y_1-Y_2|$=0.07; $MSD_{0.01[3.176]}$=0.69) and between Faxafloi and the South-Coast ($|Y_1-Y_2|$=0.79; $MSD_{0.05[3.176]}$=0.71).

No statistical comparisons were made on data from seals from the East-fjords because of too few samples. The limiting data does however, give indications of increased P. decipiens-infections from spring to the beginning of the breeding-season in the autumn. Samples from the last months of the year lack completely. Infections of C. osculatum are however, low in all samples from the East-fjords (Table 2d).

Comparisons of proportions of mature P.decipiens and C.osculatum.

The mean-proportion of mature P. decipiens decreases slightly,

but not significantly, from spring to autumn ($F_{1,171}$=3.64, p=0.06; slope=-0.20) (fig. 3,4,5). The proportions are on the other hand significantly different between areas ($F_{2,171}$=1308; p<0.001). The mean-proportion is highest in seals from the South-Coast but lower in seals from Faxafloi and Breidafjord. Comparisons of pares of the proportions show that the significance originates in the difference between the South-Coast and Faxafloi ($|Y_1-Y_2|$=0.27; $MSD_{0.01[3.176]}$=0.15) and in the difference between the South-Coast and Breidafjord ($|Y_1-Y_2|$=0.27; $MSD_{0.01[3.176]}$=0.19). The mean-proportions of mature P. decipiens did on the contrary, not variate significantly between Faxafloi and Breidafjord.

The mean-proportions of mature C. osculatum increases significantly from spring to autumn ($F_{1,171}$=5.24; p=0.02; slope=0.25) (Fig 6,7,8). The proportion is highest in seals from the South-Coast but lowest from Breidafjord. Comparisons of pares show that the significance originates in the difference between the South-Coast and Breidafjord ($|Y_1-Y_2|$=0.26; $MSD_{0.01[3.176]}$=0.15) and in the difference between Faxafloi and Breidafjord ($|Y_1-Y_2|$=0.22; $MSD_{0.01[3.176]}$=0.17).

Comparisons on anisakid-infections between surveys in 1979-82 and 1989-93.

Comparison on anisakid infections in grey-seals from Breidafjord between surveys in 1979-82 and 1989-93 did only indicate a significant increase of C. osculatum ($F_{1,129}$=10,02; p<0,01).

Discussions.

The same anisakid-species were found in the grey-seal stomachs in the present study as in earlier investigations around Iceland (3,2) and in the Northern-Atlantic Ocean (1). P. decipiens and C. osculatum are the most common species. The abundance of P. cystophorae in the seal-stomachs is nowhere high but worms of this species are usually found in great abundance in the seals' intestine (6). A. simplex worms can survive in seals for some time and their abundance can occasionally reach extreme levels. Their growth and

development in seals are however, poor. Maturity is only reached in exceptional instances and is probably intensity-depended. H. aduncum was observed in few seals. The species matures in a fish-host and does most certainly not survive for long in a digestive-tract of a warm-blooded mammal.

The intensities of anisakids follow the hosts' weight but no significant difference was found between the sexes. Stobo et. al. (7) got similar results where length of the seals explained best differences in worm-abundance but the sex only indirectly, as the sexes differ in size. A difference in infections between the sexes may however, be expected as females and males differ in behaviour, especially during the breeding-season. It is noteworthy that the males from the South-Coast are much more infected than females in September but the infections are similar in October to December. The females may come to the breeding-sites on the South-Coast and start their fast earlier than the males.

Changes in number and species-compositions of anisakids in the stomachs of grey-seals are clear in seals from Breidafjord and Faxafloi and some hints of the same can be seen from the limited data from the East-Fjords. The means of the total worm-burden increase from spring to autumn and continue to increase after the breeding has begun in October. No samples were collected from the South-Coast in the spring but in contrary to the increase in the West-Coast seals, do the means of the total worm-burden in males fall from summer to autumn.

The number of P. decipiens increases but C. osculatum decreases or remains unchanged in seals from Breidafjord and Faxafloi from spring to autumn. Hints of comparable increase in P. decipiens are visible in seals from the East-Fjords but infections of C. osculatum are always low there. Infections of both anisakid-species remain unchanged in females from the South-Coast from summer to autumn but infections of both species decrease in males.

P. decipiens and C. osculatum infections in seal-stomachs are not intensity-dependent until possibly at extreme abundance (6). The numbers of worms of these species are therefore

influenced by the diet and possibly also, by responses of the host rather than competition for space in the stomach. Investigations on the diet of Icelandic grey-seals show that they do consume some food during the breeding-season and that they prey mostly upon fishes close to the breeding-area during that time (8). The grey-seals' diet in Breidafjord during feeding-time consists mainly of Lumpsucker (Cyclopterus lumpus), Sand-eels (Ammodytes spp.) and Cod (Gadus morhua), but the importance of these species in the diet decreases during breeding and Sea-scorpions (Myoxocephalus scorpius) become prominent (8). Sea-scorpions play probably an important role too in Faxafloi, especially close to the large breeding-sites off the coasts of Myrar (unpubl. data). Sand-eels are the most common food-species in the seals' diet off the South-Coast in the autumn (unpubl. data). Investigations on nematode-infections in fishes inhabiting the coast-areas around Iceland show extremely high P. decipiens-infections in Sea-scorpions from Breidafjord and Faxafloi (9). Contracaecum sp. larvae are also found in number of fish-species but the largest infections are observed in Sand-eels.

The large numbers of P. decipiens in grey-seals from Breidafjord and Faxafloi in the autumn cause a significant difference in the total number of worms and the number of P. decipiens in these two areas in comparisons to seals from the South-Coast. This is the case even though the data from the South-Coast originate from the largest seals (table 1).

The abundance of C. osculatum was highest in seals from Breidafjord but lowest in Faxafloi. The large C. osculatum-infections in seals from the South-Coast are in an agreement with the importance of Sand-eels in the diet. The samples from the South-Coast derive from the autumn when the food consumption is low. The infections of C. osculatum in this area on a year-basis is therefore most likely underestimated.

The present results support the outcome of the earlier investigation on aniskid-infections in Icelandic seals, performed in the in the years 1979-82 (2). The number of samples in the earlier study were however, fewer and originated from a larger area than in the present study. The

sampling-area was divided into a "west-" and an "east-area". The year was divided into a "feeding-time" (Feb-Sept) and a "breeding-time" (Oct-Jan). P. decipiens-infections were significantly larger and C. osculatum-infections were significantly smaller in the "breeding-time" than in the "feeding-time". Infections of P. decipiens did not differ significantly between the "west-" and the "east-area" but C. osculatum-infections were significantly higher in the "west-area". No samples were collected from the South-Coast in the older survey and samples from the North- and the East-Coasts in the present study are sporadic. The comparisons between areas in the two surveys are therefore not fully comparable. Both investigations give however, information of the largest infections in seals from Breidafjord and Faxafloi.

P. decipiens-larvae reach maturity in 15-25 days in seals and the worms may survive up to 80 days after infection (10). The results of the proportions of mature worms in different seasons are in an agreement with expectations of lower proportions at intervals when the infections of that particular species are increasing. A consequent increase in the proportions of mature worms with declining infections is however, not equally intense. This indicates slower development of the larvae at intervals with decreased food consumption during breeding-time. Stobo et.al. (7) came to a similar conclusion. They found low proportions of mature P. decipiens in grey-seal stomachs during breeding but high proportions soon after breeding. The low proportions of mature P. decipiens in grey-seals from Faxafloi and Breidafjord in the autumn are most likely results of the large numbers of new infections but the development of these worms will probably stay slow until after breeding.

A change in the proportions of the developmental stages of P. decipiens from spring to autumn is not significant when infections from all three areas are analyzed. The decrease in the proportions of mature P. decipiens observed in Faxafloi and Breidafjord from spring to autumn become neutralized with the increase of the proportions in seals from the South-Coast. The proportions of mature C. osculatum increase, however,

significantly from spring to autumn. A significant difference in mature C. osculatum-worms was also observed between all areas. The lowest proportions in seals from Breidafjord and the highest in the South-Coast seals. This is probably because more samples from Breidafjord derive from the spring when the proportions of mature C. osculatum is lowest.

Information on influences of seal-populations-sizes on the population-sizes of anisakids are still poor. Young (11) found the largest nematode-infections in grey-seals where the grey-seal populations were greatest. Icelandic seals are also most infected of P. decipiens in areas with the largest grey-seal populations, in Faxafloi and Breidafjord. Other ecological factors in these areas are also likely to favour large nematode-populations, especially P. decipiens. A higher sea-temperature along the West- and South-Coasts of Iceland is positive for the survival and development of the young anisakid-larvae (13,14). Small depths and wide distributions of sea-weeds inhabited by large numbers of all necessary hosts for P. decipiens, are characteristic for the ecosystem of Breidafjord and large areas in Faxafloi. The role of sea-scorpions in grey-seals' diet during feeding-time seams to be of greatest importance for their infections of P. decipiens. Sea-scorpions live on crustacea and smaller fishes. The fact that the fish lives its entire life in the coastal areas and that it may reach seven years of age (14) makes it a perfect supplier of the parasite when all other ecological factors are favourable.

Sandy beaches and large depths are characteristic for the South-Coast. Seals only inhabit the sandy-South-Coast in the autumn and migrate to unknown destinations after breeding (unpubl. data). The high proportions of mature worms and poor remains of food in their stomachs (unpubl. data) indicate older infections originating from distant areas. The average sea-temperature north and east off Iceland is low (12,13). The depths are larger and distributions of grey seals are smaller than off the West-Coast (15). Distributions of C. osculatum seems to be more bound to the warmer areas off the South- and the West-Coasts than the distribution of P. decipiens. Sand-eels are important and probably the most important

intermediate host for the species.

The crater-like wounds on the stomach-wall are well known in seals and are probably caused by the frequent behaviour of the anisakids of burrowing the head into the stomach-wall(16). The burrowing worms are most frequently C. osculatum (17) but P. cystophorae is often attached to the wall of the pyloric cacea (18). P. decipiens has only been found attached to the stomach-wall in experimental infections (16). The nature behind this behaviour is not fully understood. These worms are less likely to be passively brought out of the host, with digested food or in case of weakness after prolonged fast. McClelland (16) found worms more frequently attached to the wall in empty stomachs. This however, does not explain the simultaneous behaviour of clustering on the stomach-walls. Theories relating the behaviour to the ecdysis of the larvae have also been made (16) but C. osculatum larvae and mature worms are as frequent in clusters. If the behaviour is related to the ecdysis, one would expect the worms to loosen after reaching maturity and if it is part of the mating then it's difficult to explain the number of small larvae in the clusters. McClelland (16) observed wounds more frequently in common-seals than grey-seals and that the attaching-behaviour of the worms and wounds on the stomach-walls were more frequent in experimentally infected seals than in wild individuals. He concluded that the mutual tolerance "host-parasite relationship" were more likely to be disordered in seals under pressure and in common-seals rather than in grey-seals. If this is the case, one can conclude the "host-parasite relationship" between P. decipiens and its seal-hosts to be better evolved than between C. osculatum and its seal-hosts. This also supports other indications of grey-seals being "better" hosts for P. decipiens than common-seals (10).

The clustering-behaviour of anisakids in the seal-stomachs are perhaps their response to the hosts' immunal-reactions.

References.

1 Brattey J, Stobo WT (Rapporteurs). Group report 2: Infection of definitive hosts. In: Bowen WD, ed. Population biology of sealworm (Pseudoterranova decipiens) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci.1990; 222:163-170

2 Olafsdottir D and Hauksson E. Infections of Anisakidae nematodes in Common seals (Phoca vitulina L.) and Grey seals (Halichoerus grypus Fabr.) in Icelandic waters in 1979-82. (in prep.)

3 Pálsson J. Nematode infestation and feeding habits of Icelandic seals. I.C.E.S. C.M. 1977; N:20

4 Hauksson E. Biology of common seals (Phoca vitulina L.) and grey seal (Halichoerus grypus Fabr.), length-weight relationships, growth curves and fecundity. Hafrannsóknir 1992; 43:23-49 (in icelandic: english summary)

5 Sokal RR, Rohlf CJ. Biometry (2nd). San Francisco: W.H.Freeman & Co, 1981

6 Olafsdottir D. and Hauksson E. Distributions of Anisakidae nematodes in the digestive tract of Common seals (Phoca vitulina L.) and Grey seals (Halichoerus grypus Fabr.). (in prep.)

7 Stobo WT, Beck B, Fanning LP. Seasonal sealworm (Pseudoterranova decipiens) abundance in grey seals (Halichoerus grypus). In: Bowen WD, ed. Population biology of sealworm (Pseudoterranova decipiens) in relation to its intermediate and seal hosts. Can. Bull. Fish. Aquat. Sci.1990; 222:147-162

8 Hauksson E. Um fædu útsela. In: Hersteinsson P, Sigbjarnason G, eds. Villt íslensk spendýr. Reykjavík: Hid Íslenska Náttúrufraedifélag - Landvernd, 1993: 223-226 (in icelandic)

9 Hauksson E. Larval Anisakinae nematodes in various fish species from the coast of Iceland. Hafrannsóknir 43:105-123. (in icelandic: english summary)

10 McClelland G. Phocanema decipiens: Growth, reproduction, and survival in seals. Experimental Parasitology 1980; 49:175-187

11 Young PC. The relationship between the precence of larval Anisakine nematodes in Cod and marine mammals in British home waters. J. Applied Ecology 1972; 9:459-485

12 Kristmannsson SS. Sjávarhitamælingar vid strendur Íslands 1987-88. Hafrannsóknarstofnun 1989; 17 (in icelandic)

13 Kristmannsson SS. Sjávarhitamælingar vid strendur Íslands 1989-90. Hafrannsóknarstofnun 1991; 24 (in icelandic)

14 Jónsson G. Íslenskir fiskar (2nd). Reykjavík: Fjölvi, 1992 (in icelandic)

15 Hauksson E. Íslenskir Selir. In: Hersteinsson P, Sigbjarnason G, eds. Villt íslensk spendýr. Reykjavík: Hid Íslenska Náttúrufraedifélag - Landvernd, 1993: 188-201 (in icelandic)

16 McClelland G. Phocanema decipiens: Pathology in seals. Experimental Parasitology 1980; 49:405-419

17 Young PC, Lowe D. Larval nematodes from fish of the subfamily Anisakinae and gastro-intestinal lesions in mammals. J. Comp. Path. 1969; 79:301-313

18 Berland B.. Phocascaris cystophorae sp. nov. (Nematoda) from the hooded seal with an emendation of the genus. Årbok Univ. Bergen 1963; 17:3-21.

Table 1. Mean weight values of grey-seals behind the data.

	Faxafloi	Breidafjord	South-Coast
Females (kg)	137	124	144
Number	27	63	24
Males (kg)	129	132	219
Number	6	33	26

1-4 year

Table 2a

Breidafjord		< 1 year				1-4 ára selir				> 4 + years			
	Months	Prev	Mean intensity (N samples) Larvae / fem / male			SD	Prev	Mean intensity (N samples) Larvae / fem / male		SD	Prev	Mean intensity (N samples) Larvae / fem / male		SD
All Species Females	Jan-Mars													
	Apr-June	100	1319,33		(6)	413,65	100	1306,67	(3)	561,67	100	1594,09	(11)	748,64
	July-Sept	100	1317,50		(2)	840,75	100	739,80	(5)	279,29	100	1066,29	(7)	722,94
	Oct-Des						100	882,50	(2)	386,74	100	3211,70	(27)	3826,59
All species Males	Jan-Mars	-	1614,00		(1)	-								
	Apr-June	100	1927,08		(12)	1308,21	100	1209,00	(2)	620,84				
	July-Sept						100	1579,83	(6)	1090,14	100	2104,00	(9)	962,62
	Oct-Des										100	1023,67	(3)	751,55
P.decipiens Females	Jan-Mars													
	Apr-June	100	225,67 /	56,67 /	64,00	123,86 / 45,00 / 51,22	100	338,67 /	94,67 / 157,33	242,86 / 33,55 / 22,75	100	141,00 /	66,73 / 74,54	111,45 / 36,84 / 40,40
	July-Sept	100	357,00 /	72,50 /	101,00	502,05 / 10,61 / 72,12	100	143,40 /	80,60 / 100,20	95,39 / 89,10 / 97,09	100	185,14 /	83,71 / 96,86	122,13 / 74,28 / 67,02
	Oct-Des						100	688,50 /	45,00 / 74,00	395,27 / 4,24 / 19,80	100	2288,52 /	213,15 / 363,70	3234,88 / 253,79 / 554,54
P.decipiens Males	Jan-Mars	-	12,00 /	15,00 /	10,00	-								
	Apr-June	100	387,33 /	84,83 /	105,83	373,35 / 93,85 / 105,81	100	137,00 /	104,00 / 66,00	145,66 / 124,45 / 76,37				
	July-Sept						100	447,17 /	121,00 / 159,17	513,21 / 91,39 / 187,67	100	336,00 /	126,33 / 127,78	409,91 / 66,34/ 61,09
	Oct-Des										100	769,67 /	66,67 / 99,67	581,29 / 43,15 / 20,24
C.osculatum Females	Jan-Mars													
	Apr-June	100	579,33 /	127,00 /	130,00	353,60 / 58,57 / 61,49	100	486,67 /	117,33 / 89,33	222,07 / 93,84 / 72,04	100	805,36 /	149,27 / 130,36	747,20 / 111,32 / 113,33
	July-Sept	100	378,00 /	28,50 /	13,00	393,15 / 17,68 / 7,07	100	180,80 /	73,40 / 70,60	97,58 / 29,83 / 19,59	100	536,00 /	65,14 / 62,86	637,82 / 51,77 / 51,59
	Oct-Des						100	27,00 /	15,00 / 11,00	26,87 / 4,24 / 7,07	100	235,63 /	50,81 / 47,22	440,50 / 59,86 / 58,81
C.osculatum Males	Jan-Mars	-	211,00 /	10,00 /	10,00	-								
	Apr-June	100	715,67 /	231,92 /	285,00	383,87 / 257,04 / 319,04	100	570,00 /	144,00 / 154,00	65,05 / 90,51 / 110,31				
	July-Sept						100	551,50 /	136,67 / 137,33	471,67 / 168,33 / 187,41	100	534,78 /	168,78 / 184,67	365,15 / 92,31 / 102,12
	Oct-Des										100	77,33 /	3,00 / 5,67	67,28 / 4,36 / 8,96
P.cystophorea Females	Jan-Mars													
	Apr-June	33.33	1,33 /	0,00 /	0,00	2,06 / 0,00 / 0,00	66.67	0,00 /	14,67 / 1,33	0,00 / 16,17 / 2,31	63.64	11,55 /	3,36 / 2,82	33,51 / 5,77 / 3,43
	July-Sept	100	6,00 /	3,00 /	3,50	8,48 / 4,24 / 4,95	40	0,40 /	2,40 / 1,40	0,89 / 5,37 / 3,13	42.87	0,29 /	1,43 / 0,00	0,76 / 2,99 / 0,00
	Oct-Des						100	13,00 /	4,00 / 2,00	18,38 / 5,66 / 2,83	22.22	0,44 /	5,15 / 0,37	2,31 / 13,63 / 1,36
P.cystophorea Males	Jan-Mars	-	356,00 /	8,00 /	4,00	-								
	Apr-June	8.33	0,00 /	5,33 /	4,00	0,00 / 18,47 / 13,86	50	5,00 /	11,00 / 16,00	7,07 / 7,07 / 11,31				
	July-Sept						0	0,00 /	0,00 / 0,00	0,00 / 0,00 / 0,00	22.22	0,89 /	0,00 / 1,77	2,67 / 0,00 / 5,33
	Oct-Des										33.33	0,00 /	0,67 / 0,00	0,00 / 1,15 / 0,00
Contracaecum sp Phocascaris sp Females	Jan-Mars													
	Apr-June	16.67	106,00			166,77	0	0,00		0,00	27.27	176,82		410,62
	July-Sept	100	178,00			251,73	0	0,00		0,00	14.27	5,14		13,61
	Oct-Des						0	0,00		0,00	0	0,00		0,00
Contracaecum sp Phocascaris sp Males	Jan-Mars	-	968,00			-								
	Apr-June	33.33	85,17			179,87	50	75,00		106,01				
	July-Sept						0	0,00		0,00	11.11	1,33		4,00
	Oct-Des										0	0,00		0,00
A.simplex ' Females	Jan-Mars													
	Apr-June	66.67	29,33 /	0,00		60,27 / 0,00	66.67	5,33 /	1,33	4,62 / 2,31	63.64	14,91 /	16,27	21,99 / 29,92
	July-Sept	100	97,00 /	8,00		66,47/ 11,31	20	4,00 /	37,60	54,04 / 84,08	57.14	27,43 /	2,29	49,54 / 6,05
	Oct-Des						100	3,00 /	0,00	1,41 / 0,00	37.04	6,56 /	0,15	12,34 / 0,77
A.simplex ' Males	Jan-Mars	-	0,00 /	0,00		-								
	Apr-June	58.33	15,33 /	6,66		38,01 7 23,09	50	2,00 /	0,00	2,83 / 0,00				
	July-Sept						100	27,00 /	0,00	34,59 / 0,00	88.89	367,67 /	224,00	433,10 / 672,00
	Oct-Des										33.33	1,00 /	0,00	1,73 / 0,00
H.aduncum Females	Jan-Mars													
	Apr-June	0	0,00			0,00	0	0,00		0,00	0	0,00		0,00
	July-Sept	0	0,00			0,00	0	0,00		0,00	0	0,00		0,00
	Oct-Des						0	0,00		0,00	0	0,00		0,00
H.aduncum Males	Jan-Mars	-	0,00			-								
	Apr-June	0	0,00			0,00	0	0,00		0,00				
	July-Sept						0	0,00		0,00	0	0,00		0,00
	Oct-Des										0	0,00		0,00

Table 2b

Faxaflói		< 1 year			1-4 ára selir			> 4 + years		
	Months	Prev	Mean intensity (N samples) Larvae / fem / male	SD	Prev	Mean intensity (N samples) Larvae / fem / male	SD	Prev	Mean intensity (N samples) Larvae / fem / male	SD
All Species Females	Jan-Mars				-		-	-	3509,00 (1)	-
	Apr-June				-	305,00 (1)		100	1006,17 (6)	989,66
	July-Sept				100	1145,00 (2)	1028,13	100	1438,42 (7)	1494,96
	Oct-Des							100	5816,00 (10)	6575,77
All species Males	Jan-Mars	-	28,00 (1)	-				-	408,00 (1)	-
	Apr-June	-	610,00 (1)	-				-	674,00 (1)	-
	July-Sept				-	316,00 (1)	-	-	1488,00 (1)	-
	Oct-Des									
P.decipiens Females	Jan-Mars							-	288,00 / 53,00 / 117,00	-
	Apr-June				-	166,00 / 23,00 / 23,00	-	100	342,67 / 162,67 / 182,17	618,72 / 163,54 / 185,67
	July-Sept				100	796,00 / 51,00 / 131,00	1091,77 / 26,87 / 18,38	100	612,71 / 187,71 / 252,86	875,73 / 242,39 / 370,33
	Oct-Des							100	4872,50 / 238,60 / 344,50	6237,94 / 175,69 / 303,03
P.decipiens Males	Jan-Mars	-	22,00 / 0,00 / 1,00	-				-	162,00 / 52,00 / 60,00	-
	Apr-June	-	36,00 / 2,00 / 12,00	-				-	124,00 / 40,00 / 42,00	-
	July-Sept				-	100,00 / 86,00 / 88,00	-	-	264,00 / 36,00 / 76,00	-
	Oct-Des									
C.osculatum Females	Jan-Mars							-	0,00 / 0,00 / 0,00	-
	Apr-June				-	14,00 / 14,00 / 11,00	-	100	63,00 / 73,00 / 42,67	58,01 / 72,74 / 38,76
	July-Sept				100	96,00 / 19,00 / 17,00	33,94 / 4,24 / 24,04	100	101,71 / 61,29 / 58,14	58,13 / 62,84 / 48,46
	Oct-Des							80	135,20 / 78,50 / 63,40	157,19 / 103,28 / 112,66
C.osculatum Males	Jan-Mars	-	1,00 / 0,00 / 1,00	-				-	66,00 / 26,00 / 28,00	-
	Apr-June	-	38,00 / 60,00 / 52,00	-				-	24,00 / 96,00 / 94,00	-
	July-Sept				-	0,00 / 8,00 / 2,00	-	-	744,00 / 68,00 / 68,00	-
	Oct-Des									
P.cystophorea Females	Jan-Mars							-	1237,00 / 0,00 / 0,00	-
	Apr-June				-	6,00 / 2,00 / 4,00	-	100	4,00 / 14,50 / 16,00	6,32 / 11,73 / 9,21
	July-Sept				100	4,00 / 6,00 / 9,00	5,66 / 8,49 / 12,73	85.71	0,57 / 19,00 / 10,57	0,00 / 25,46 / 20,02
	Oct-Des							0	0,00 / 0,00 / 0,00	0,00 / 0,00 / 0,00
P.cystophorea Males	Jan-Mars	-	0,00 / 0,00 / 0,00	-				-	0,00 / 0,00 / 0,00	-
	Apr-June	-	6,00 / 38,00 / 52,00	-				-	20,00 / 18,00 / 12,00	-
	July-Sept				-	0,00 / 8,00 / 12,00	-	-	12,00 / 4,00 / 0,00	-
	Oct-Des									
Contracaecum sp Phocascaris sp Females	Jan-Mars							-	1685,00	-
	Apr-June				-	41,00	-	50	41,50	82,19
	July-Sept				0	0,00	0,00	28.57	84,00	164,10
	Oct-Des							20	71,80	158,96
Contracaecum sp Phocascaris sp Males	Jan-Mars	-	0,00	-				-	0,00	-
	Apr-June	-	138,00	-				-	104,00	-
	July-Sept				-	0,00	-	-	124,00	-
	Oct-Des									
A.simplex ° Females	Jan-Mars							-	128,00 / 0,00	-
	Apr-June				-	1,00 / 0,00	-	100	66,83 / 0,83	98,31 / 2,04
	July-Sept				100	16,00 / 0,00	22,63 /	71.43	12,29 / 37,00	17,30 / 89,71
	Oct-Des							10	11,50 / 0,00	36,37 / 0,00
A.simplex ° Males	Jan-Mars	-	3,00 / 0,00	-				-	14,00 / 0,00	-
	Apr-June	-	176,00 / 0,00	-				-	12,00 / 88,00	-
	July-Sept				-	12,00 / 0,00	-	-	92,00 / 0,00	-
	Oct-Des									
H.aduncum Females	Jan-Mars							-	0,00	-
	Apr-June				-	0,00	-	0	0,00	0,00
	July-Sept				0	0,00	0,00	14.29	0,57	1,51
	Oct-Des							0	0,00	0,00
H.aduncum Males	Jan-Mars	-	0,00	-				-	0,00	-
	Apr-June	-	0,00	-				-	0,00	-
	July-Sept				-	0,00	-	-	0,00	-
	Oct-Des									

Table 2c

South-Coast	Months	< 1 year Prev	< 1 year Mean intensity (N samples) Larvae / fem / male	< 1 year SD	1-4 åra sellr Prev	1-4 åra sellr Mean intensity (N samples) Larvae / fem / male	1-4 åra sellr SD	> 4 + years Prev	> 4 + years Mean intensity (N samples) Larvae / fem / male	> 4 + years SD
All Species Females	Jan-Mars	-			-		-	-	2812,00 (1)	-
	Apr-June							100	4066,67 (3)	3986,17
	July-Sept					628 (1)		100	580,78 (9)	440,05
	Oct-Des							100	670,20 (10)	1002,12
All species Males	Jan-Mars	-	480,00 (1)	-				-	998,00 (1)	-
	Apr-June									
	July-Sept							100	1892,50 (18)	1961,13
	Oct-Des							100	407,83 (6)	205,40
P.decipiens Females	Jan-Mars	-			-		-	-	40,00 / 24,00 / 72,00	-
	Apr-June							100	224,00 / 12,00 / 29,33	55,45 / 12,00 / 20,13
	July-Sept					116,00 / 184,00 / 172,00		100	100,89 / 97,77 / 109,44	199,87 / 108,11 / 113,51
	Oct-Des							100	149,70 / 50,30 / 92,00	265,70 / 66,30 / 118,57
P.decipiens Males	Jan-Mars	-	4,00 / 2,00 / 0,00	-				-	146,00 / 32,00 / 18,00	-
	Apr-June									
	July-Sept							100	312,50 / 303,22 / 343,00	373,33 / 397,36 / 441,65
	Oct-Des							100	47,50 / 24,17 / 29,17	22,85 / 22,08 / 20,24
C.osculatum Females	Jan-Mars	-			-		-	-	48,00 / 12,00 / 8,00	-
	Apr-June							100	334,67 / 94,67 / 134,67	267,74 / 121,74 / 188,48
	July-Sept					20,00 / 60,00 / 32,00		100	55,56 / 96,00 / 84,22	60,18 / 131,82 / 108,33
	Oct-Des							100	191,20 / 76,20 / 79,70	457,13 / 94,10 / 90,05
C.osculatum Males	Jan-Mars	-	0,00 / 0,00 / 0,00	-				-	72,00 / 16,00 / 0,00	-
	Apr-June									
	July-Sept							100	375,17 / 146,72 / 176,89	589,66 / 171,82 / 262,80
	Oct-Des							100	101,00 / 87,33 / 97,50	160,17 / 72,43 / 94,24
P.cystophorea Females	Jan-Mars	-			-		-	-	416,00 / 0,00 / 0,00	-
	Apr-June							100	906,67 / 48,00 / 61,33	848,20 / 69,74 / 80,13
	July-Sept					0,00 / 4,00 / 0,00		33.33	1,11 / 1,11 / 0,67	3,33 / 2,67 / 1,41
	Oct-Des							80	0,30 / 2,40 / 1,10	0,67 / 2,59 / 2,51
P.cystophorea Males	Jan-Mars	-	452,00 / 12,00 / 6,00	-				-	0,00 / 0,00 / 0,00	-
	Apr-June									
	July-Sept							55.55	13,22 / 3,78 / 3,56	33,29 / 8,08 / 8,67
	Oct-Des							83.33	3,17 / 3,50 / 7,33	2,71 / 6,32 / 10,11
Contracaecum sp Phocascaris sp Females	Jan-Mars	-			-		-	-	2072,00	-
	Apr-June							66.67	2066,67	3558,81
	July-Sept					0,00		0	0,00	0,00
	Oct-Des							0	0,00	0,00
Contracaecum sp Phocascaris sp Males	Jan-Mars	-	0,00	-				-	0,00 / 0,00 / 0,00	-
	Apr-June									
	July-Sept							0	0,00	0,00
	Oct-Des							16.67	7,17	17,55
A.simplex ° Females	Jan-Mars	-			-		-	-	120,00 / 552,00	-
	Apr-June							66.67	89,33 / 65,33	96,69 / 96,36
	July-Sept					8,00 / 32,00		77.78	7,22 / 21,89	13,61 / 23,54
	Oct-Des							20	6,50 / 20,80	20,21 / 65,77
A.simplex ° Males	Jan-Mars	-	4,00 / 0,00	-				-	160,00 / 554,00	-
	Apr-June									
	July-Sept							83.33	56,44 / 158,06	136,33 / 212,10
	Oct-Des							0	0,00 / 0,00	0,00
H.aduncum Females	Jan-Mars	-			-		-	-	0,00	-
	Apr-June							0	0,00	0,00
	July-Sept					0,00		11.11	4,33	13,00
	Oct-Des							0	0,00	0,00
H.aduncum Males	Jan-Mars	-	0,00	-				-	0,00 / 0,00	-
	Apr-June									
	July-Sept							0	0,00	0,00
	Oct-Des							0	0,00	0,00

Table 2d

East-fjords	Months	< 1 year Prev	< 1 year Mean intensity (N samples) Larvae / fem / male	< 1 year SD	1-4 ára selir Prev	1-4 ára selir Mean intensity (N samples) Larvae / fem / male	1-4 ára selir SD	> 4 + years Prev	> 4 + years Mean intensity (N samples) Larvae / fem / male	> 4 + years SD
All Species Females	Jan-Mars Apr-June July-Sept Oct-Des	-	158,00 (1)	-				100 100	318,16 (6) 1457,75 (4)	244,04 1093,32
All species Males	Jan-Mars Apr-June July-Sept Oct-Des	-	269,00 (1)	-				-	2315,00 (1)	-
P.decipiens Females	Jan-Mars Apr-June July-Sept Oct-Des	-	72,00 / 17,00 / 21,00	-				100 100	85,67 / 46,50 / 47,00 1183,00 / 98,75 / 128,00	92,03 / 37,41/ 38,69 1118,34 / 114,11 / 135,92
P.decipiens Males	Jan-Mars Apr-June July-Sept Oct-Des	-	13,00 / 683,00 / 736,00	-				-	757,00 / 20,00 / 16,00	-
C.oeculatum Females	Jan-Mars Apr-June July-Sept Oct-Des	-	12,00 / 6,00 / 7,00	-				100 50	24,50 / 18,33 / 13,83 4,75 / 2,00 / 0,25	25,58 / 17,33 / 15,01 7,63 / 4,00 / 3,77
C.oeculatum Males	Jan-Mars Apr-June July-Sept Oct-Des	-	115,00 / 4,00 / 11,00	-				-	0,00 / 43,00 / 53,00	-
P.cystophorea Females	Jan-Mars Apr-June July-Sept Oct-Des	-	2,00 / 0,00 / 1,00	-				100 25	16,66 / 13,67 / 10,50 0,75 / 0,75 / 0,00	31,24 / 17,68 / 15,91 1,50 / 1,50 / 0,00
P.cystophorea Males	Jan-Mars Apr-June July-Sept Oct-Des	-	5,00 / 2,00 / 0,00	-				-	0,00 / 0,00 / 0,00	-
Contracaecum sp Phocascaris sp Females	Jan-Mars Apr-June July-Sept Oct-Des	-	0,00 / 0,00 / 0,00	-				33.33 0	29,33 0,00	69,91 0,00
Contracaecum sp Phocascaris sp Males	Jan-Mars Apr-June July-Sept Oct-Des	-	16,00	-				-	0,00	-
A.simplex * Females	Jan-Mars Apr-June July-Sept Oct-Des	-	20,00 / 0,00	-				83.33 100	9,00 / 2,83 4,50 / 32,50	6,32 / 4,66 4,12 / 32,02
A.simplex * Males	Jan-Mars Apr-June July-Sept Oct-Des	-	67,00 / 0,00	-				-	43,00	-
H.aduncum Females	Jan-Mars Apr-June July-Sept Oct-Des	-	0,00	-				16.67 0	0,33 0,00	0,82 0,00
H.aduncum Males	Jan-Mars Apr-June July-Sept Oct-Des	-	0,00	-				-	0,00	-

Table 2e

North-Coast	< 1 year				1-4 ára selir			> 4 + years		
	Months	Prev	Mean intensity (N samples) Larvae / fem / male	SD	Prev	Mean intensity (N samples) Larvae / fem / male	SD	Prev	Mean intensity (N samples) Larvae / fem / male	SD
All Species Females	Jan-Mars Apr-June July-Sept Oct-Des	100	257,50 (2)	167,58						
P.decipiens Females	Jan-Mars Apr-June July-Sept Oct-Des	100	156,50 / 8,50 / 21,00	140,71 / 0,71 / 9,90						
C.osculatum Females	Jan-Mars Apr-June July-Sept Oct-Des	100	18,50 / 13,50 / 12,00	14,85 / 17,68 / 16,97						
***P.cystophorae* Females**	Jan-Mars Apr-June July-Sept Oct-Des	50	0,00 / 1,00 / 1,00	0,00 / 1041 / 1,41						
Contracaecum sp Phocascaris sp Females	Jan-Mars Apr-June July-Sept Oct-Des	0	0,00	0,00						
A.simplex * Females	Jan-Mars Apr-June July-Sept Oct-Des	100	25,50 / 0,00	4,95 / 0,00						
H.aduncum Females	Jan-Mars Apr-June July-Sept Oct-Des	0	0,00	0,00						

* Nematodes identified to larvae and adult worms

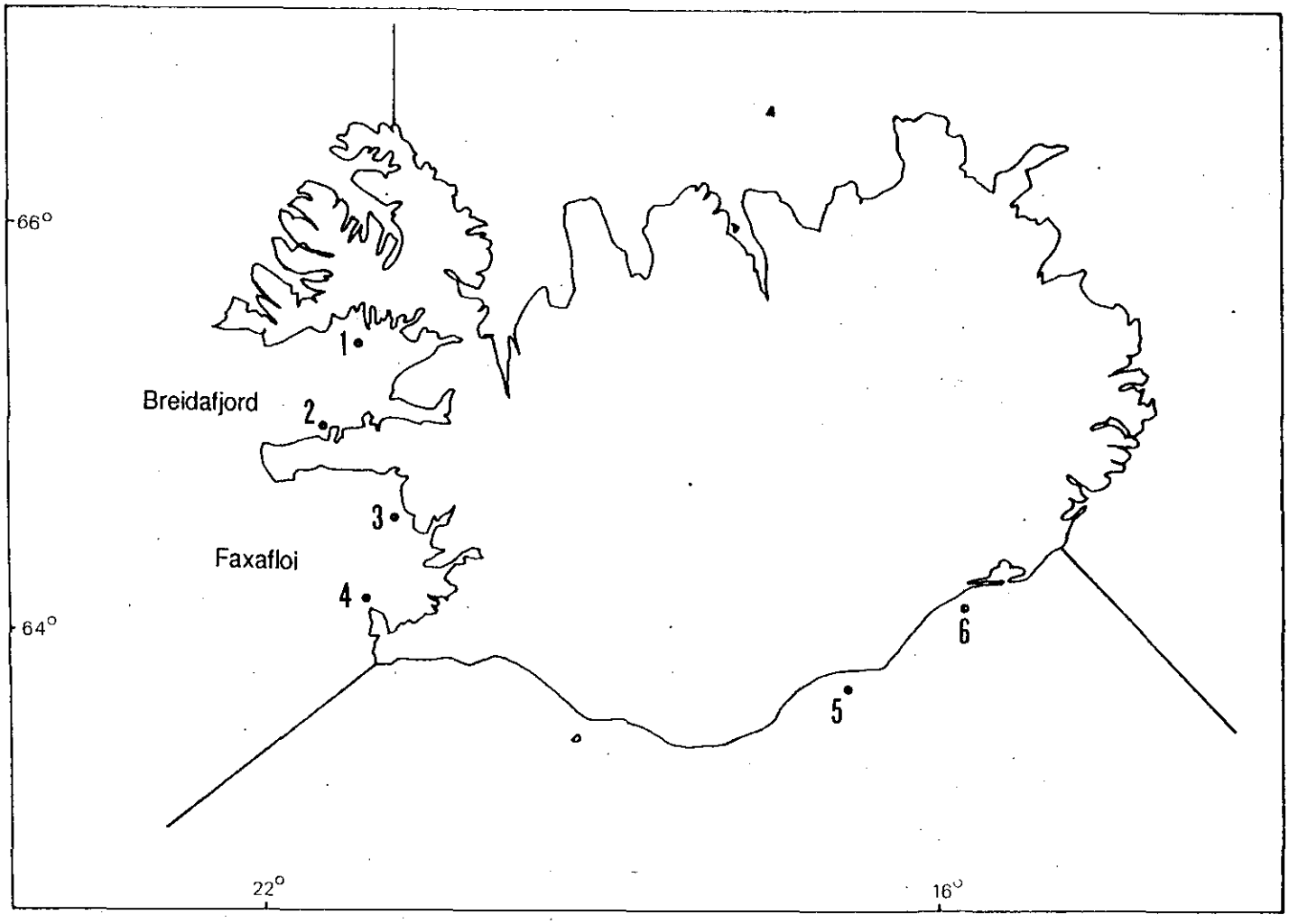

Fig. 1. Sites of grey seal sampling 1989-93, Breidafjord: Flatey (1), North-coast of Snaefellsnes (2); Faxafloi: Myrar (3), Gardskagi (4); South-Coast: Skeidararsand (5), Sudursveit (6); East-Fjords: Bakkafjord (7); North-Coast: Siglufjord (8).

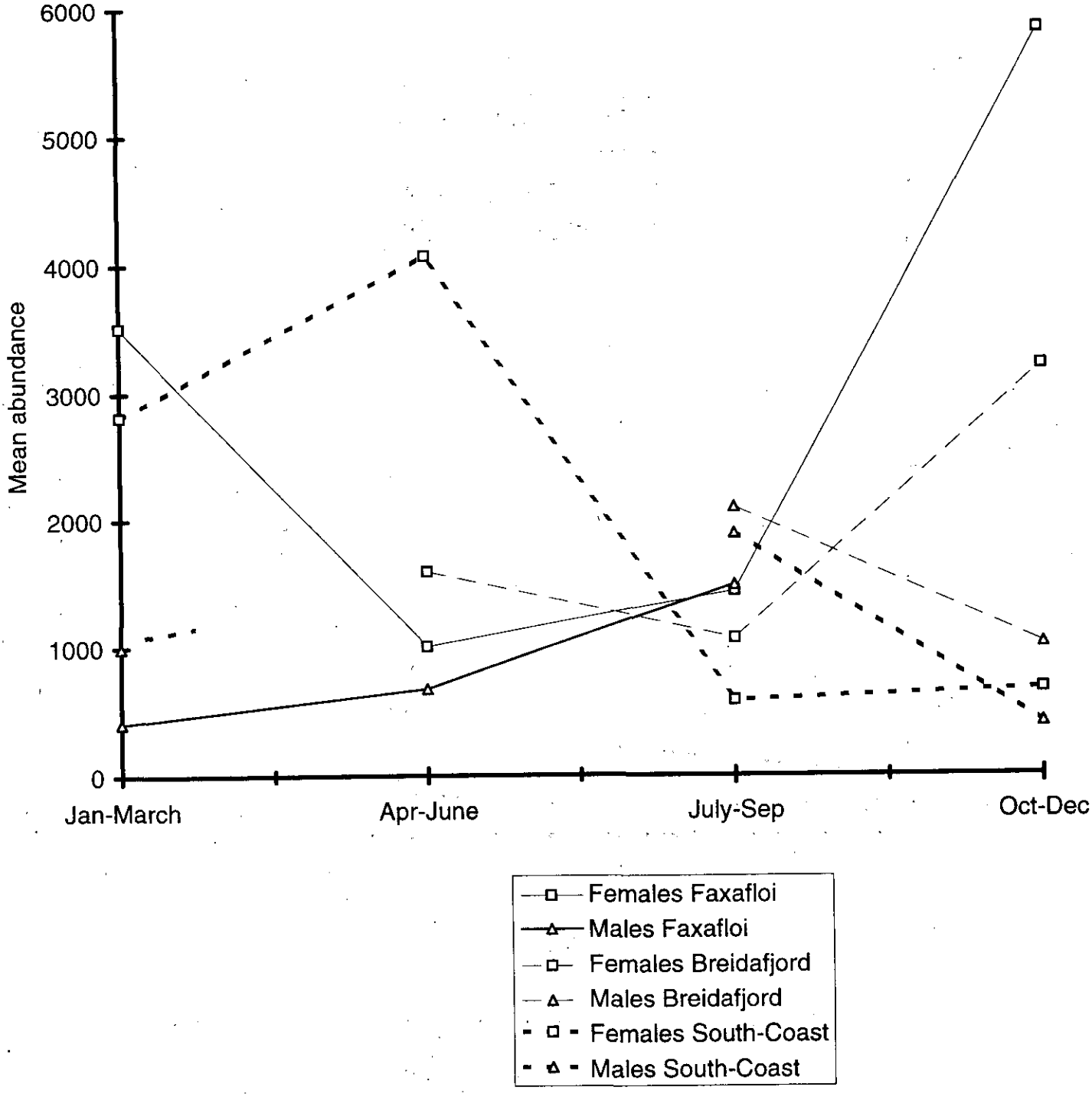

Fig. 2. Seasonal changes in mean abundance of nematodes in stomachs of females and males of 5 years and older grey seals from Faxafloi, Breidafjord and the South-coast of Iceland in 1989-93.

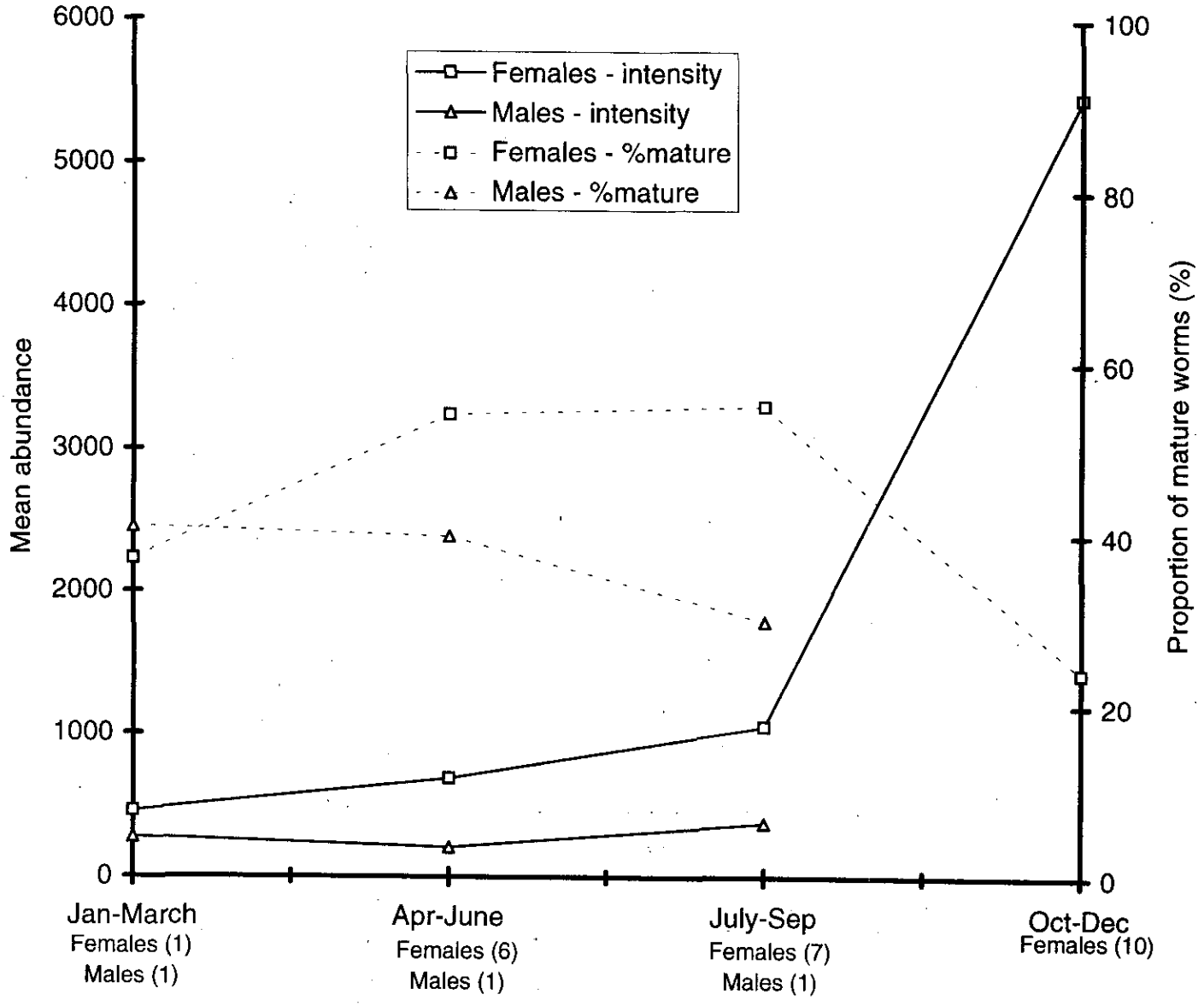

Fig. 3. Seasonal changes in mean abundance and proportions of mature worms of P.decipiens in stomachs of females and males of 5 years and older grey seals from Breiðafjord in 1989-93.

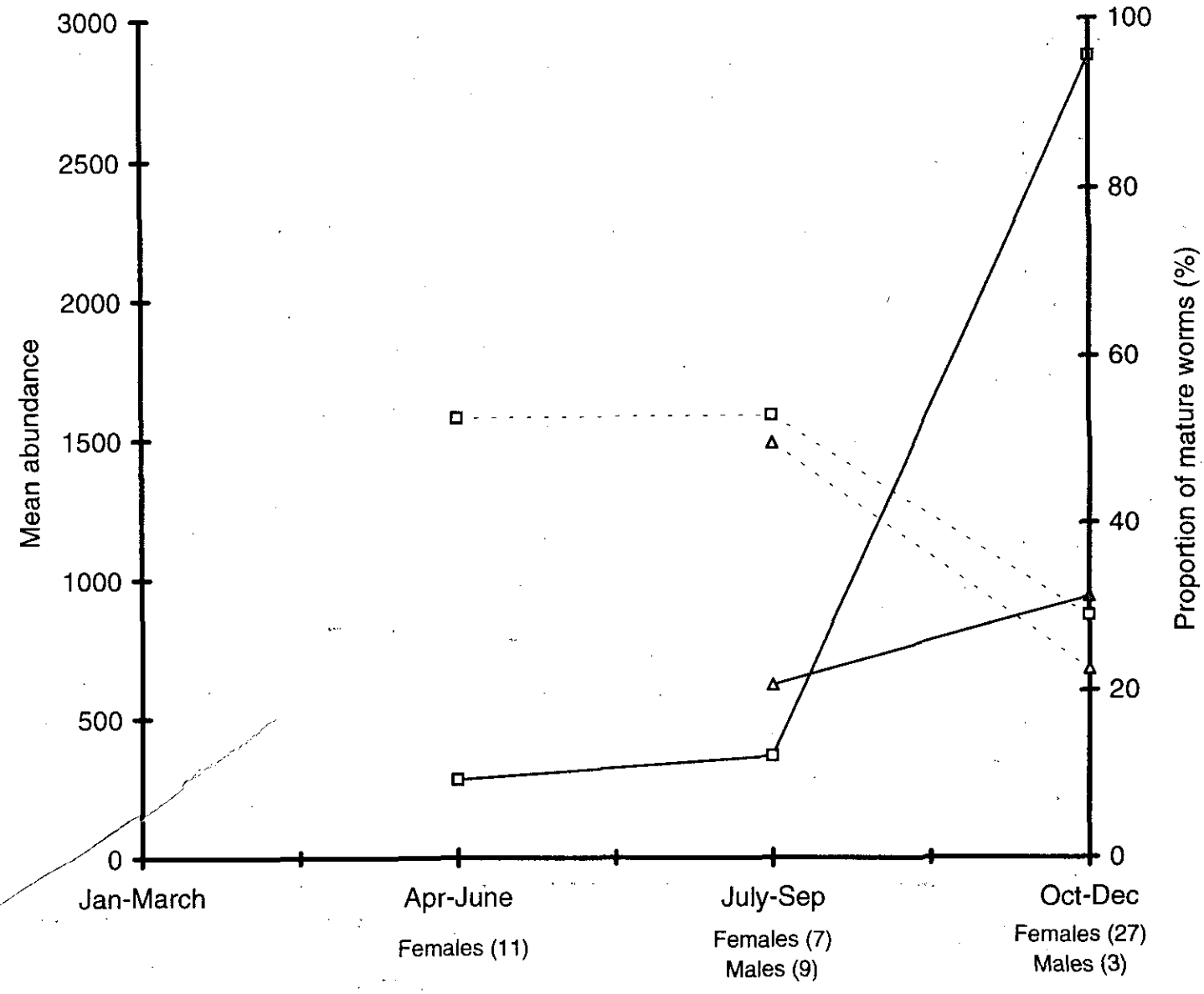

Fig. 4. Seasonal changes in mean abundance and proportions of mature worms of P.decipiens in stomachs of 5 years and older grey seals from Faxafloi in 1989-93.

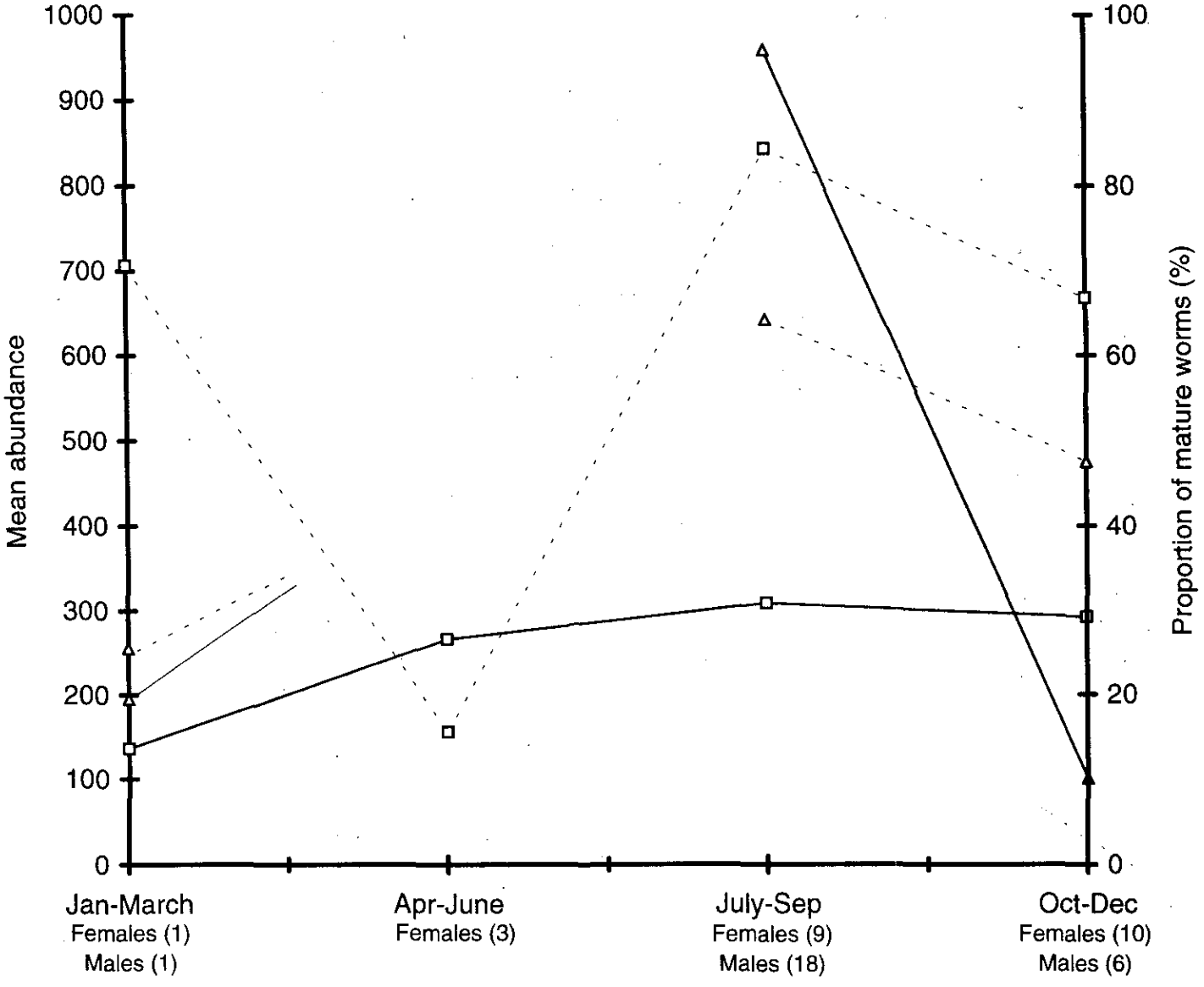

Fig. 5. Seasonal changes in mean abundance and proportions of mature worms of P.decipiens in stomachs of females and males of 5 years and older grey seals from the South-coast of Iceland in 1989-93.

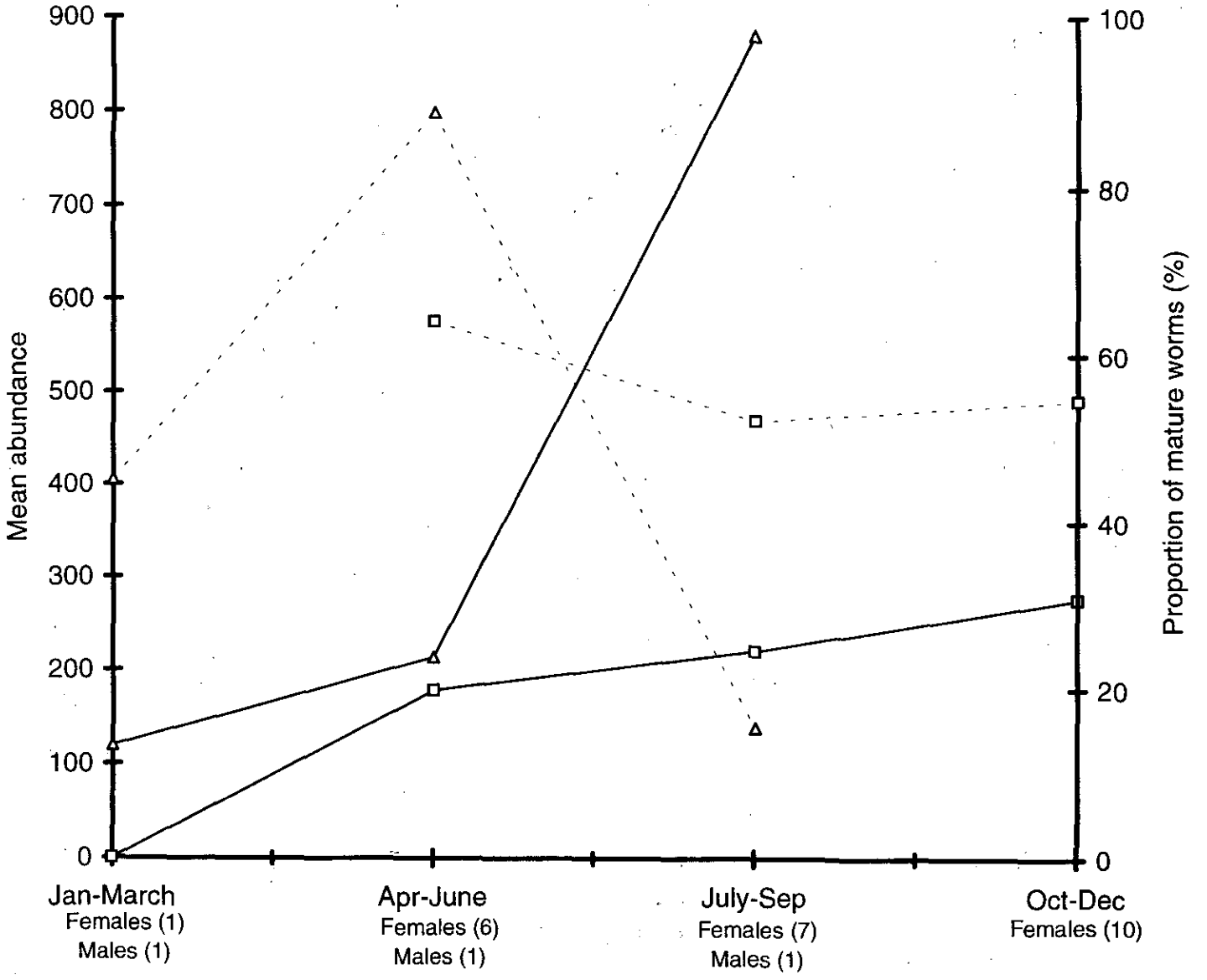

Fig. 6. Seasonal changes in mean abundance and proportions of mature worms of C.osculatum in stomachs of females and males of 5 years and older grey seals from Breiðafjord in 1989-93.

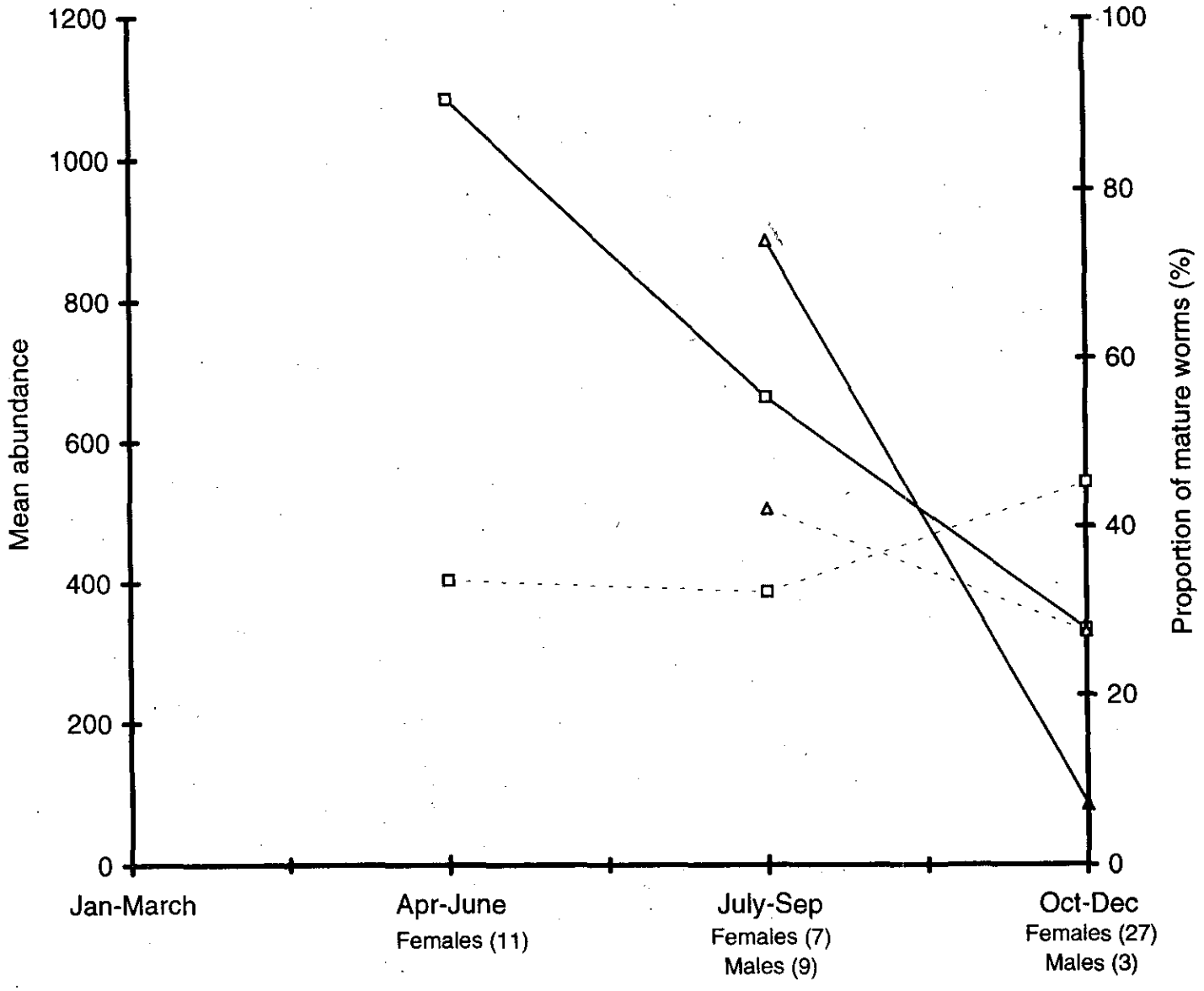

Fig. 7. Seasonal changes in mean abundance and proportions of mature worms of C.osculatum in stomachs of females and males of 5 years and older grey seals from Faxafloi in 1989-93.

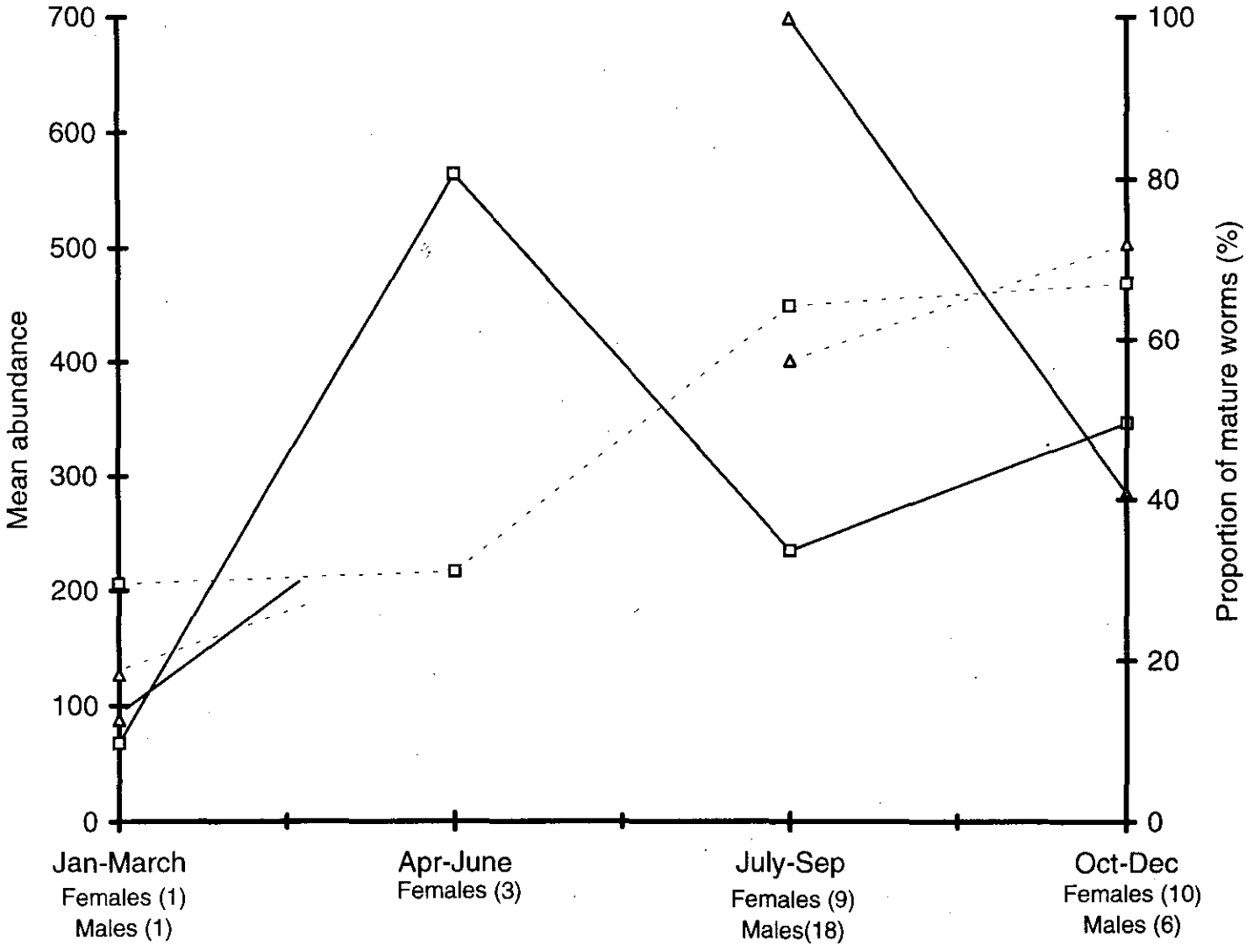

Fig. 8. Seasonal changes in mean abundance and proportions of mature worms of C.osculatum in stomachs of females and males of 5 years and older grey seals from the South-coast of Iceland in 1989-93.