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Distribution and seasonal prevalence of *Hematodinium* sp. infection of the Norway lobster (*Nephrops norvegicus*) around the west coast of Scotland

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Around Scotland, coastal stocks of the commercially important Norway lobster (*Nephrops norvegicus*), particularly those within the Clyde Sea Area (CSA), have for some years been known to be infected by syndiniid dinoflagellate endoparasites of the genus *Hematodinium*. The prevalences of infected Norway lobsters in trawl samples from the CSA are reported for 1992–1995, together with similar data from a range of Scottish west coast sites in 1992, and from the Irish Sea in 1994 and 1995. In the CSA, infection prevalences declined after 1992 and were higher than those recorded in other sampled areas. Infection by *Hematodinium* was confined to the first half of the year, peaking in the spring and early summer, with medium-sized and female lobsters showng the highest prevalence. Comparison between CSA sites suggests that infection may be influenced by factors directly related to *Nephrops* age rather than size. In addition to the usual diel variability in catch, in spring male *Nephrops* showed diel variability in *Hematodinium* prevalence in trawl samples (being higher in the midnight samples). Females showed no diel variation in prevalence. Underwater television surveys of *Nephrops* burrow density and data on commercial landings indicate a decrease in *Nephrops* abundance in the last decade, which might in part reflect the higher levels of infection by *Hematodinium* during this time.

Key words: *Nephrops norvegicus*, *Hematodinium*, lobster, sydiniid, Clyde Sea Area, Scotland.

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Introduction

The infection of *Nephrops norvegicus* (hereafter referred to by genus) by a syndiniid parasite dinoflagellate of the genus *Hematodinium* has been known since the mid-1980s (Field *et al.*, 1992). Similar *Hematodinium* spp. have been shown to have serious consequences for their host decapod populations (Shields, 1994), infection probably being fatal to the majority of hosts. Studies of geographically widespread *Hematodinium* spp. infections have suggested a number of environmental and host-intrinsic factors in the transmission of these pathogens. The foremost factor amongst those identified as having a role in pathogen transmission is moult (Meyers *et al.*, 1987; Field *et al.*, 1992; Messick, 1994). *Nephrops* catches vary with light intensity (Atkinson and Naylor, 1976; Chapman, 1980) and light-dependent behaviour may be influenced by *Hematodinium* infection.

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In the present paper we present information on prevalence levels of *Hematodinium* sp. within *Nephrops* populations from the Scottish west coast and Irish Sea waters, especially in relation to host *Nephrops* population factors such as age/size structure, moulting, and diel variability in catch. Since *Hematodinium* prevalences are higher in the Clyde than elsewhere, mortality due to *Hematodinium* infection is therefore likely to be best reflected in the Clyde fishery data. Such data, together with underwater television assessments of *Nephrops* density were therefore examined.

Methods

Survey techniques

From April 1992 to March 1995 samples of *Nephrops norvegicus* were collected by trawl at sites within the Clyde Sea Area (CSA) and around the Scottish west coast using the vessel RV "Aora", supplementing previously published data collected using the same techniques in 1991 (Field *et al*., 1992). The trawl used was a Marine Laboratory Aberdeen type BT 126D (22 mm mesh size with a codend of 12 mm mesh). Samples were also collected at sites in the Irish Sea using a custom-made *Nephrops* net (43.2 ± 1.25 mm mesh size with a codend of 48.7 ± 1.57 mm mesh size) from the RV "Lough Foyle" in April 1994 and April 1995 (see Figs 1 and 2). Certain sites within the CSA were sampled regularly (see Table 1), whilst west coast and other sites were sampled only once, in May 1992, or infrequently. Sampling at each site was by trawls of 1 h duration. Weighed subsamples (approximately 5 kg) were examined, carapace length (CL), and sex recorded, together with moult stage (by pleopod examination after Aiken, 1980). Disease status was then assigned (using a four-point scale after Field *et al*., 1992 and Field and Appleton, 1995, see below), by the removal and microscopical examination of a pleopod from each lobster in order to categorize parasite density within the haemolymph. From these data, infection prevalences within each sample were calculated in relation to sex and moult status. Moult was described as either premoult or intermoult, since postmoult is not reliably distinguishable from intermoult by the Aiken (1980) method. Depth, time, and latitude and longitude of the start and finish of each haul were recorded.

Assessment of reliability of diagnosis and survey techniques

Disease prevalence estimates, made by two field workers, were compared in March 1994; a sample of 77 adult *Nephrops* caught by trawling at the South of Little Cumbrae site (Fig. 1) was examined; each animal was inspected and a pleopod assessment of both moult stage and disease status was made independently by each observer.

Analyses of CSA survey data

Statistical analyses of prevalence survey data were made using the Minitab package. In addition, data were studied on disease prevalence, diagnosed by pleopod examination, with respect to time of year, size, and sex using generalized linear modelling (GLM) in Genstat (Table 1). *Nephrops* size distributions were broken down into 10 mm length groups, starting at carapace length group 10–19 mm, up to 60–69 mm. Diseased *Nephrops* were allotted to one of four severity states (after Field *et al*., 1992, stage IV being the most severe) and one of three moult stages, corresponding to Stage 0 (intermoult: includes animals in postmoult), Stages 1.0–2.5 (passive premoult) and Stages 3.0–5.5 (active premoult) (Aitken, 1980).

Diel variability in *Hematodinium* prevalence

The degree to which time of day affected prevalence was assessed by a series of diel sampling regimes conducted at the South of Little Cumbrae site (Site 1, Fig. 1, depth ca. 70 m) on the 8–9 March, 7–11 April, and 10–11 May, 1995 from the RV "Aora". Each monthly survey consisted of a total of five trawl samples, each of 1 h duration, trawl start times (GMT) were mid-morning (0930 ± 1 h), noon (1200 ± 1.0), dusk (1730 ± 1, except May 1940), midnight (0000 ± 0.5) and dawn (0630 ± 1, except May 0345). Trawling was conducted at approximately similar states of tide. Catches were sampled and examined using the same protocol as for routine survey samples.

Assessment of *Nephrops* burrow density

An underwater TV (UWTV) low light-sensitive colour camera (model OE1362, Simrad Osprey Electronics, Aberdeen, UK) with a fixed focal length standard lens and wide field of view was mounted on a sledge together with underwater lights. This was towed astern of the RV "Aora" at sites in the CSA (see Table 2), using a trawl warp to which the electrical cables of the camera and lights were attached by quick-release ties. When positioned on the sledge the camera looked obliquely forwards. Speed and position of RV "Aora" were recorded and the output from the TV camera was recorded on videotape (VHS), together with a time signal.

Individual *Nephrops* burrow systems (see Atkinson and Nash, 1985; Atkinson, 1986; Atkinson and Taylor, 1988, 1991 for identification) were counted as they

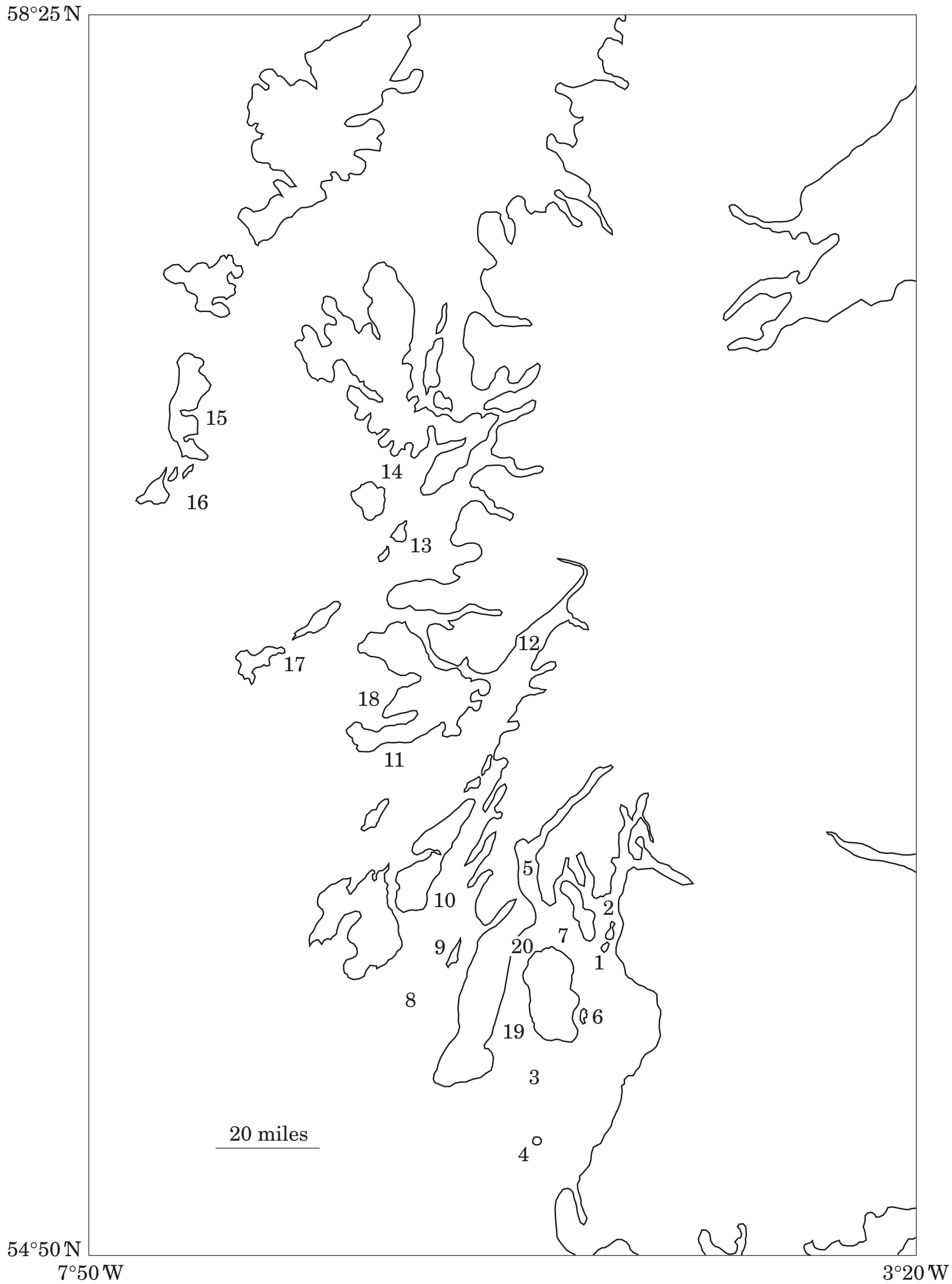

Figure 1. Map of west coast of Scotland showing surveyed sites (sites 1–7, 19 and 20 in Clyde Sea Area; sites 8–10 in Sound of Jura, site 12 Loch Linnhe, sites 11, 13, 14, 17 and 18 Inner Hebrides and sites 15 and 16 in Outer Hebrides).

passed a line of known width (usually 80 cm) drawn across the screen of a TV monitor, one-third up from the bottom of the display. The area of seabed viewed (m^2) was computed from the length of the tow and the field width; burrow density was computed from the burrow count and area of seabed viewed.

CSA and Sound of Jura landings and effort data

Commercial catches of *Nephrops* from the Sound of Jura (Fig. 1, in region of tows sites 8–10) and CSA since 1979 were obtained from Fisheries Research Services, Aberdeen. From these data, yearly landings per unit

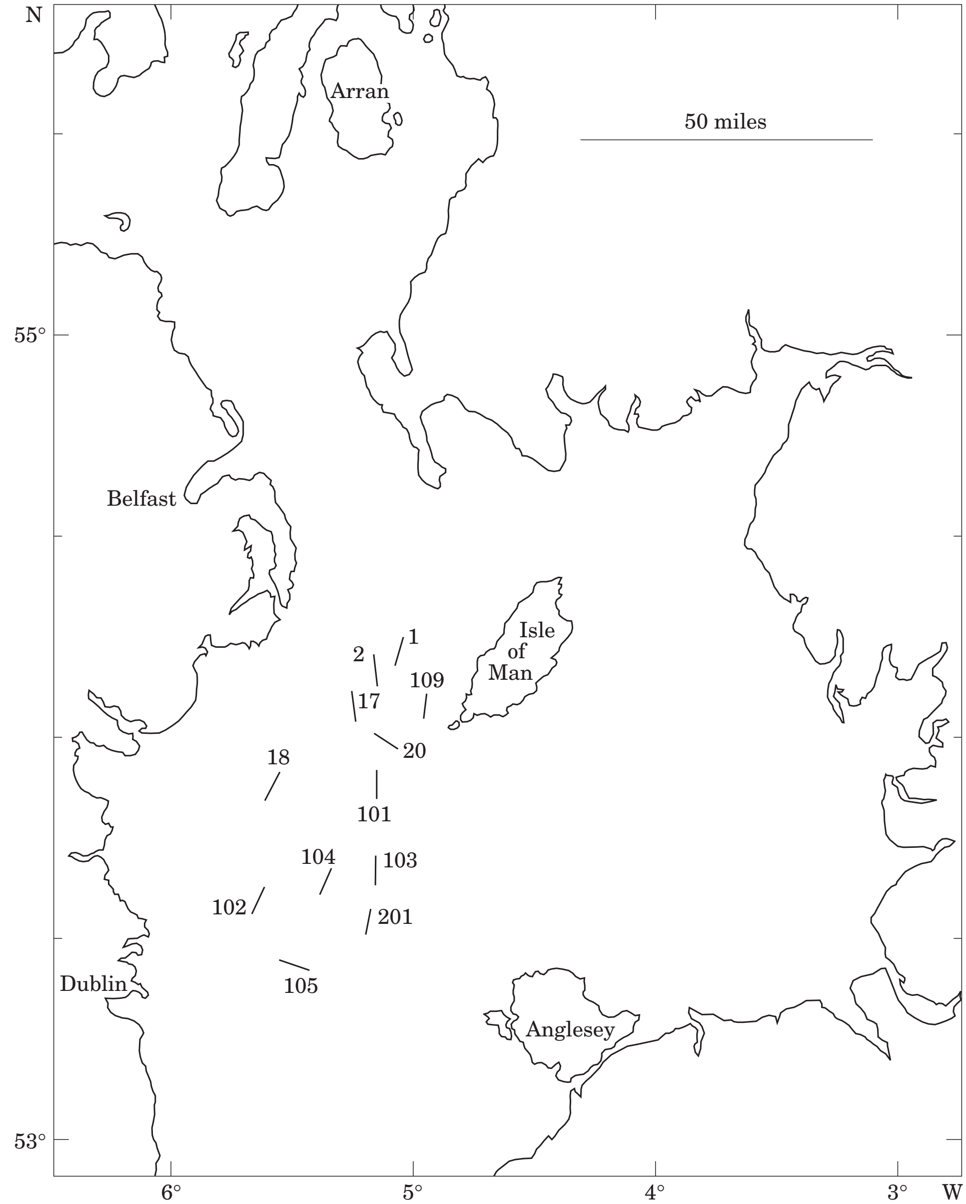

Figure 2. Map showing the sites surveyed in the Irish Sea.

effort were calculated for both areas. *Nephrops* single trawls were the most common gear type used; data for landings by light trawls and *Nephrops* multi-trawls (introduced in 1991) have not been included in analyses to maintain consistency.

Results

Assessment of the reliability of diagnosis and survey techniques

Although there was some disagreement between the categorization of moult stages and severity of infection for individual *Nephrops*, the overall prevalence recorded within the 77 animals of the subsample by each of the two investigators was the same (18.2%). These figures indicate that prevalence estimates made by both workers were comparable.

Prevalence survey of the CSA and Scottish west coast

Infected *Nephrops* were found at all sites surveyed in the CSA and in Scottish west coast inshore waters as far north and west as the east coast of the Outer Hebrides

Table 1. Sites, months, and years of regular samples of *Hematodinium* prevalence in Clyde Sea Area *Nephrops* included in generalized linear modelling, during 1991–1993. Site numbers correspond to those in Fig. 1.

Year	Month	Sites
1991*	3	1,2,3,5,7
1992	4	1,2,3,4,5,6,7
	5	1,2,3,4,5,6,7
	6	1,2,3,4,5,6,7
	7–12	1,2,3,4,5,6,7
1993	2	1,3,4,5,6,7
	3	1,2,3,4,6,7

*Including data from previous study, Field *et al.*, 1992.

(Fig. 1, sites 15 and 16). Prevalences from trawls varied between 0 and 60%. However, in general, the prevalences recorded outside the Clyde were much lower than those in *Nephrops* populations in the CSA (Tables 3 and 4).

A strong seasonality of prevalence was observed throughout the period of this study (Table 3). Infections were evident in samples taken at the site South of Little Cumbrae (Fig. 1, site 1) in January 1992 with prevalence at around 30% (Table 3), suggesting that the disease reappeared in late 1991. Maximum prevalences recorded at most sites within the CSA in 1992–1994 (with the exception of Loch Fyne and Holy Isle) decreased compared with those recorded previously (Field *et al.*, 1992), but still remained considerably higher than those observed at west coast sites. In contrast, the majority of sites investigated on west coast grounds in 1992 exhibited prevalences above those previously reported, although it must be noted that the prevalences were recorded in different months of the year.

Reappearance of the disease on Clyde grounds began in December 1992, at very low prevalences, and continued to increase through the spring of 1993. Sampling was less frequent in late 1993/early-1994 but infection was clearly present in January 1994 samples. These re-appearances seem to have followed the pattern of previous years.

Reliable estimates of prevalences in the Irish Sea were made in April 1994 and 1995. Although the gear used was of a larger mesh size, both in the trawl body and the codend, than that used in CSA and west coast sampling, the Irish Sea samples were much greater in weight and number of lobsters caught. *Hematodinium* infections were observed in *Nephrops* in every sample examined (Table 4). The range of prevalences encountered in these samples was within the range observed in the CSA in 1994 and 1995.

Comparison of *Hematodinium* infection prevalence in populations of differing size distributions

South of Little Cumbrae (Site 1, Fig. 1), infection was present in males between 24 and 48 mm CL and in females of between 24 and 44 mm CL (Fig. 3a and b). In males (Fig. 3a) the distribution of infection with relation to size showed that prevalence was approximately simlar throughout most of the range of CL, the higher prevalences being restricted to the range 28–43 mm. In females (Fig. 3b), however, high prevalence levels were recorded only in the size range 28–38 mm CL.

At the site South of Ailsa (Site 4, Fig. 1) disease prevalence was in the size range 18–40 mm CL for male *Nephrops* and 18–33 mm CL for females (Fig. 3c and d).

Table 2. The results of the 1992 TV sledge survey of *Nephrops* sampling sites involved in the geographical survey detailed above. Densities are expressed both as numbers per area (top figure) and the mean area per burrow/*Nephrops* (bottom figure); site numbers correspond to those given in Fig. 1.

Site	*Nephrops* burrow density	Observed *Nephrops* density	Date and time (BST)	Area viewed
1. S. Cumbraes	$0.034 \cdot m^{-2}$	$0.004 \cdot m^{-2}$	9/6/92	2816 m^2
	1:29 m^2	1:235 m^2	1642–1840 h	
2. Main Channel	$0.024 \cdot m^{-2}$	$0.0035 \cdot m^{-2}$	25/8/92	2891 m^2
	1:41 m^2	1:289 m^2	1352–1508 h	
3. S. Arran	$0.127 \cdot m^{-2}$	$0.0076 \cdot m^{-2}$	24/8/92	1185 m^2
	1:8 m^2	1:132 m^2	1720–1742 h	
4. S. Ailsa	$0.328 \cdot m^{-2}$	$0.026 \cdot m^{-2}$	24/8/92	3224 m^2
	1:3 m^2	1:38 m^2	1410–1553 h	
5. Loch Fyne	$0.077 \cdot m^{-2}$	$0.0019 \cdot m^{-2}$	9/6/92	3112 m^2
	1:13 m^2	1:519 m^2	1117–1340 h	
6. Holy Isle	$0.046 \cdot m^{-2}$	$0.0066 \cdot m^{-2}$	25/8/92	1216 m^2
	1:22 m^2	1:152 m^2	1022–1100 h	

Table 3. The prevalence (%) *Hematodinium* infection (as diagnosed by body colour and pleopod methods) present in small mesh trawl samples of *Nephrops* taken in 1992, 1993, and 1994 at sites in the Clyde Sea Area, and around the west coast of Scotland in 1992 (site numbers correspond to those shown in Fig. 1). M=males; F=females; M and F=overall; P=premoult; I=intermoult.

Site	Date	Prevalence M	Prevalence F	Prevalence M and F	Prevalence P	Prevalence I
1. S. Cumbraes	14/1/92	37.9	47.9	40.0	—	—
1. S. Cumbraes	12/2	30.3	49.5	36.8	—	—
1. S. Cumbraes	17/3	42.6	66.7	50.3	—	—
1. S. Cumbraes	13/4	27.0	75.5	40.2	0	42.4
2. Main Channel	13/4	60.8	6.6	16.9	50.0	60.0
3. S. Arran	14/4	33.3	85.7	41.9	25.0	46.2
4. S. Ailsa	14/4	53.1	53.1	53.1	46.8	55.2
5. L. Fyne	15/4	41.4	76.9	46.9	56.3	44.8
6. Holy Isle	29/4	55.3	59.2	57.3	43.6	58.4
7. Inchmarnock	29/4	57.5	63.6	59.7	44.4	60.0
4. S. Ailsa	11/5	53.5	52.5	52.9	51.6	54.3
3. S. Arran	11/5	44.5	37.4	40.7	35.7	41.7
6. Holy Isle	12/5	40.2	42.9	44.8	—	—
7. Inchmarnock	12/5	48.8	47.8	32.6	30.0	45.6
5. L. Fyne	12/5	44.7	23.1	28.6	37.5	40.4
5. L. Fyne	13/5	39.2	37.5	27.9	33.3	37.7
1. S. Cumbraes	13/5	37.3	63.4	45.9	75.0	43.4
2. Main Channel	13/5	19.5	61.5	30.1	—	—
8. S. Snd. Jura	26/5	13.8	13.9	13.9	9.3	14.9
9. C. Snd. Jura	26/5	19.0	14.5	16.3	11.9	17.1
10. N. W. Gigha	26/5	19.7	22.3	21.3	4.1	23.6
11. Ross of Mull	27/5	19.4	32.2	25.0	22.6	25.4
12. L. Linnhe	27/5	36.0	28.6	32.0	25.5	34.2
13. Maxwell Bank	28/5	23.0	8.3	14.2	7.7	13.9
14. N. Rhum	28/5	13.1	14.1	13.8	7.3	25.4
15. E. S. Uist	29/5	14.6	17.2	16.3	5.4	17.4
16. E. Barra	29/5	9.5	17.1	13.9	14.3	13.9
17. E. Tiree	30/5	3.1	4.5	3.7	0	4.4
18. S. Staffa	30/5	7.7	6.3	7.2	4.8	7.3
19. Kilbrannan Snd. S.	1/6	35.3	55.0	48.6	0	45.9
3. S. Arran	1/6	23.8	43.8	32.4	0	37.5
4. S. Arran	1/6	22.2	7.9	13.3	6.7	14.1
6. Holy Isle	2/6	25.0	0	12.5	33.3	0
Ayr Bay	2/6	18.2	17.6	17.9	0	18.5
5. L. Fyne	2/6	30.4	33.3	31.3	0	22.6
20. Kilbrannan Snd. N.	3/6	41.3	34.0	38.5	37.5	38.6
7. Inchmarnock	3/6	33.3	50.0	40.0	0	40.0
1. S. Cumbraes	4/6	0	28.6	20.0	0	20.0
2. Main Channel	4/6	36.4	36.4	36.4	66.7	20.0
2. Main Channel	7/7	2.9	3.3	3.1	0	3.7
1. S. Cumbraes	7/7	6.5	0	3.3	0	4.0
7. Inchmarnock	7/7	5.1	3.5	4.2	0	4.5
5. L. Fyne	7–8/7	4.0	0	3.3	0	3.8
6. Holy Isle	8/7	12.5	0	9.4	0	10.0
Turnberry	8/7	0	28.6	18.2	0	22.2
3. S. Arran	8/7	5.9	0	2.7	0	2.9
4. S. Ailsa	9/7	5.3	3.3	4.4	0	4.7
2. Main Channel	17/8	7.7	33.3	20.0	0	20.0
1. S. Cumbraes	17/8	7.1	8.6	8.1	7.7	8.1
7. Inchmarnock	17/8	0	0	0	0	0
5. L. Fyne	17/8	0	0	0	0	0
3. S. Arran	18/8	1.4	0	0.9	3.2	1.1
4. S. Ailsa	18/8	0	0	0	0	0
7. Inchmarnock	21/9	0	0	0	0	0
1. S. Cumbraes	21/9	0	0	0	0	0
2. Main Channel	21/9	0	0	0	0	0
1. S. Cumbraes	19/10	0	0	0	0	0
2. Main Channel	19/10	0	0	0	0	0
7. Inchmarnock	10/10	0	0	0	0	0

Table 3. *Continued*

Site	Date	Prevalence M	Prevalence F	Prevalence M and F	Prevalence P	Prevalence I
1. S. Cumbraes	26/11	0	0	0	0	0
7. Inchmarnock	26/11	0	0	0	0	0
1. S. Cumbraes	16/12	0	0	0	0	0
2. Main Channel	16/12	0	0	0	0	0
7. Inchmarnock	16/12	3.0	0	2.4	4.5	2.0
1. S. Cumbraes	27/1/93	11.1	33.3	14.3	12.5	16.7
2. Main Channel	27/1	0	0	0	0	0
7. Inchmarnock	27/1	16.7	0	16.7	0	16.7
5. L. Fyne	16/2	0	0	0	0	0
3. S. Arran	16/2	10.3	23.1	7.1	14.8	14.2
4. S. Ailsa	15/2	4.8	8.7	5.7	5.6	5.7
6. Holy Isle	15/2	5.9	0	5.2	10.0	4.0
1. S. Cumbraes	12/2	2.2	0	1.8	0	2.3
7. Inchmarnock	12/2	10.3	33.3	13.7	27.8	10.7
6. Holy Isle	25/3	0	0	0	0	0
4. S. Ailsa	25/3	11.3	7.7	10.0	7.1	9.7
3. S. Arran	25/3	11.8	29.4	14.2	0	16.2
7. Inchmarnock	24/3	19.6	35.7	22.9	9.1	25.4
1. S. Cumbraes	24/3	8.3	21.4	10.8	0	11.3
2. Main Channel	24/3	0	0	0	0	0
1. S. Cumbraes	7/2/94	11.9	15.0	13.2	—	—
1. S. Cumbraes	14/2	18.3	19.0	18.4	—	—
1. S. Cumbraes	9/3	7.7	—*	—*	—	—
1. S. Cumbraes	23/3	7.3	—*	—*	—	—
1. S. Cumbraes	12/5	20.8	—*	—*	—	—

*Numbers of animals caught too small to make a prevalence estimate.

Table 4. Prevalence (%) of *Hematodinium* infection in trawl samples of *Nephrops* caught at sites in the western Irish Sea in April 1994 and 1995. Sites are numbered as in Fig. 2.

Site	Date	Prevalence male	Prevalence female	Prevalence overall	Total weight (kg)	No. animals
1	19/4/94	7.9	11.8	9.6	182.3	20 229
1	10/4/95	10.4	16.7	13.4	230.2	21 500
2	18/4/94	5.5	8.0	6.7	123.3	15 105
7	11/4/95	15.1	19.6	16.6	36.1	2140
8	21/4/94	8.0	9.0	8.4	37.9	3759
8	12/4/95	7.2	6.2	6.8	139.6	13 170
17	19/4/94	5.2	7.9	6.3	17.6	1625
20	19/4/94	11.0	21.9	15.8	62.9	5982
101	19/4/94	12.6	27.8	17.9	12.4	828
103	20/4/94	2.9	8.8	4.7	5.9	297
104	20/4/94	5.2	8.6	6.7	47.4	4201
105	20/4/94	7.3	6.6	7.0	108.0	11 179
105	12/4/95	10.9	13.2	11.8	170.6	10 863
106	20/4/94	2.0	4.4	3.2	23.4	2647
106	12/4/95	7.5	12.3	9.7	40.4	3345
109	11/4/95	8.9	15.5	11.5	106.0	7800
201	13/4/95	8.4	28.3	11.6	86.3	4432

Within these ranges, higher prevalences were observed between 18–32 mm CL in males and 22–32 mm CL in females. This illustrates, more markedly than at Site 1, the truncated size distribution of infected females. These data also illustrate a marked difference in the range of sizes at which the disease occurs between the two sites, infection being prevalent in larger animals at Site 1 in the north CSA than at Site 4 in the south.

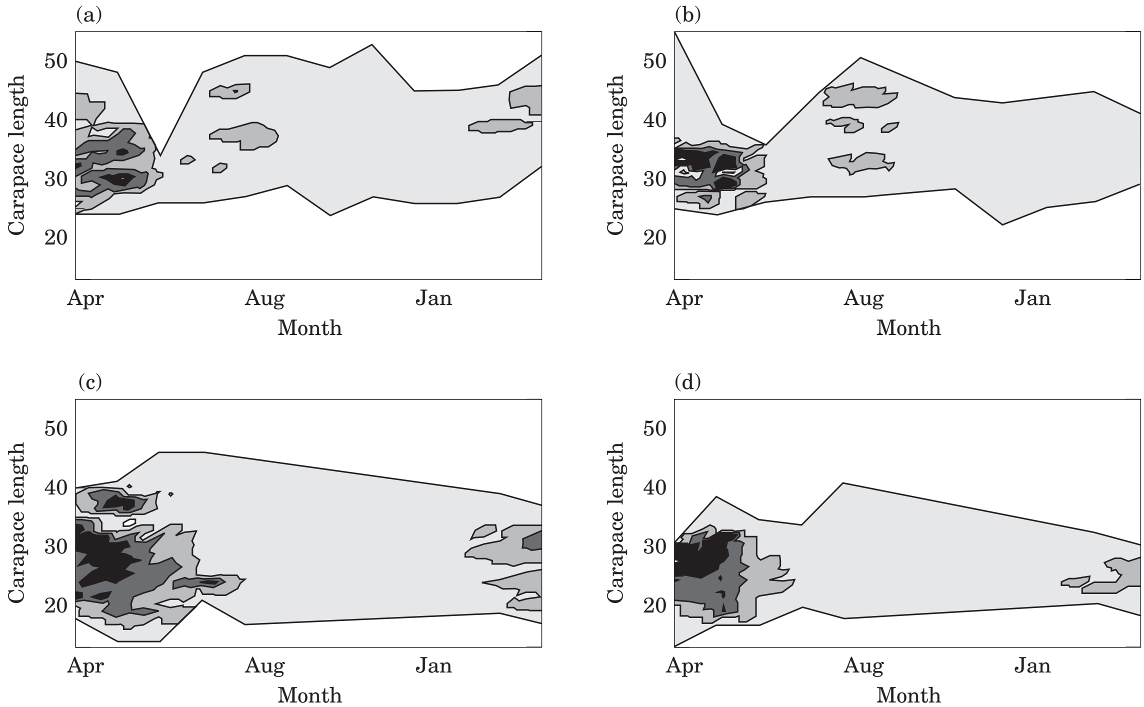

Figure 3. Graphs describing the relationship between prevalence of *Hematodinium* infection and host size (carapace length [mm]) over the course of a year (April 1992 to March 1993) for: (a) males South of Little Cumbrae, site 1 (b) females, South of Little Cumbrae, site 1; (c) males South of Ailsa Craig, site 4; and (d) females, South of Ailsa Craig, site 4. Outer contour lines bounding 0% area defines the size range of animals caught in experimental catches. 0% (□); 1–20% (□); 21–40% (▦); 41–100% (■).

Generalized linear modelling of *Hematodinium* infection of *Nephrops*

The factor that explained the greatest amount of the variation in disease prevalence in the GLM analysis was month (explaining over 70% of the total deviance), confirming the seasonal nature of appearance of the disease. Prevalences increased from the start of the year to reach their highest levels in April/May and then decreased rapidly, being only rarely evident in the latter half of the year. Size accounted for some 3% of the variability in disease prevalence. The GLM confirmed the strong seasonal expression of *Hematodinium* infection but did not reveal further factors that could explain the differences in the observed prevalences.

Diel variation in *Hematodinium* prevalence

Chi-squared analyses were carried out using bulked trawl data (March, April, and May, 1995; Table 5) to test the null hypotheses that the time of day when trawling occurred did not affect the number of animals (males and females considered separately) caught per 1 h trawl. The null hypothesis was rejected for both males (χ^2=26.6, d.f.=4, p<0.001) and females (χ^2=51.0, d.f.=4, p<0.001), suggesting that time of trawling had an effect on the total catch. In each of the months investigated, the trawl samples showed a reduction in the number of *Nephrops* caught during the hours of darkness (Table 5 and Fig. 4). Emergence activity of the *Nephrops* (as indicated by their availability for capture) tended to be lowest around midnight with the number of individuals (males and females) caught at midnight being between 6 and 57% of those caught mid-morning (Table 5). This is indicative of the diel activity patterns that have previously described for *Nephrops* (Atkinson and Naylor, 1976; Chapman, 1980).

Further chi-squared analyses were carried out to test the null hypotheses that time of day when trawling occurred had no effect on the degree of *Hematodinium* prevalence in the samples in both females and males. The results showed that time of trawling affected the degree of *Hematodinium* prevalence for males (χ^2=11.81, d.f.=4, p<0.05) but not for females (χ^2=7.13, d.f.=4, p>0.05). The significant effect of time of trawling on prevalence for males was weak with the χ^2 value of the data (11.81) being slightly larger than the p<0.05 critical value of 9.49 (d.f.=4). Prevalence in the males was highest during the midnight trawls (Table 5) indicating that infected male *Nephrops* tended to be out of their burrows more during darkness compared with uninfected males.

Table 5. Diel variation of *Hematodinium* prevalence (%) and catch (total number of *Nephrops* caught for a 1 h trawl sample) in samples of *Nephrops* taken at the same site (South of the Cumbraes; Site 1, Fig. 1) in the Clyde Sea Area for March, April, and May 1995.

Month	Sex		Time: Mid-morning	Noon	Dusk	Midnight	Dawn
March	Male	Catch	927	587	142	57	581
		Prevalence	5.7	6.8	4.9	8.8	12.1
	Female	Catch	844	730	98	43	638
		Prevalence	10.8	6.3	8.2	32.6	19.3
April	Male	Catch	243	36	19	96	69
		Prevalence	20.3	19.4	31.6	29.2	17.4
	Female	Catch	187	21	5	43	32
		Prevalence	27.3	23.8	40	25.6	21.9
May	Male	Catch	180	108	278	101	312
		Prevalence	12.2	12.5	14.1	17.8	21.2
	Female	Catch	90	63	101	45	177
		Prevalence	11.1	19	23.9	22.2	20.3

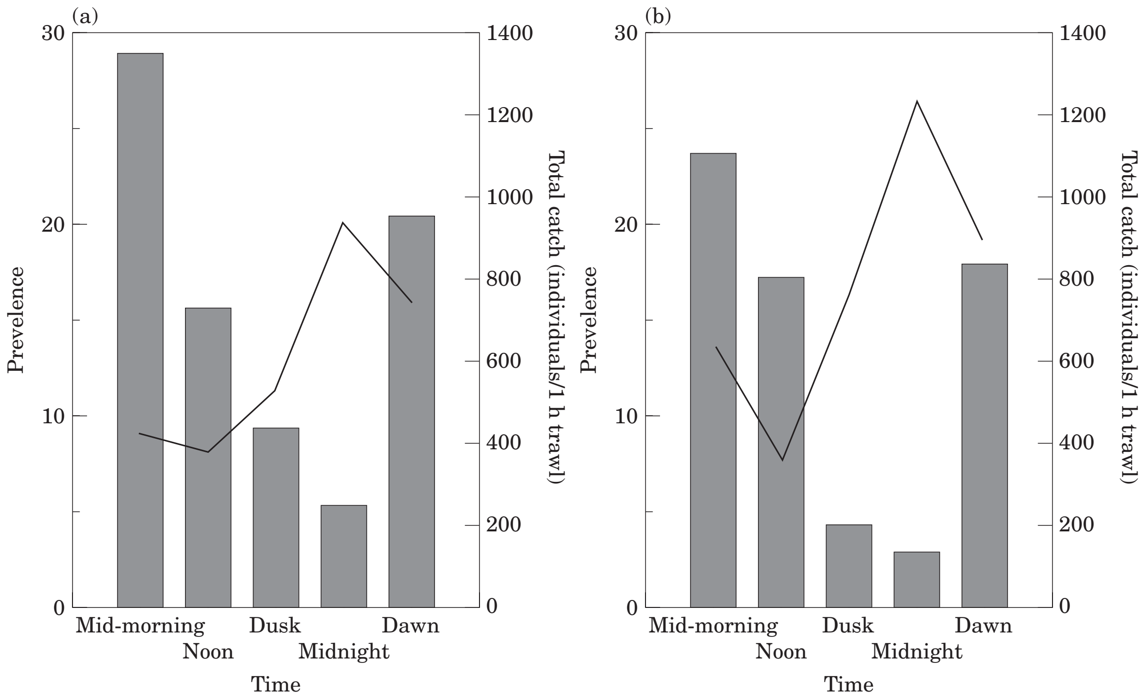

Figure 4. Graphs showing diel variation in total catch (numbers of animals per 1 h standard trawl) (▤) and *Hematodinium* prevalence (——) (%) for trawls from spring 1995; (a) males and (b) females.

Assessment of *Nephrops* burrow density

Burrow densities at six sites, varied from 0.024 to 0.328 m^{-2} (Table 2). Signs of recent trawling were evident at sites 2, 3, 4, and 6, but not at sites 1 and 5 since the Clyde fleet were mostly working west of the Kintyre peninsula at the time that these two surveys were carried out. UWTV surveys did not reveal large numbers of dead animals on the sediment surface. A small number of dead or damaged animals were observed, but this is perfectly normal on trawled grounds. *Nephrops* burrow densities were, however, substantially lower than those recorded in previous studies at several sites on CSA *Nephrops* grounds (Table 6).

CSA and Sound of Jura landings and effort data

Mean commercial landings per unit effort (LPUE) of *Nephrops* caught in the Sound of Jura (outside the CSA)

Table 6. *Nephrops* burrow densities (burrow systems · m^{-2}) for CSA stations in various years. Data are derived from the following sources: 1970 from Chapman (1979); 1980/81 from Bailey and Chapman (1983); 1991 from Tuck (1993); 1992 this study; 1993 from IMBC, UMBSM, and IRPEM (1994). NB: the site referred South of Ailsa Craig marked * different to site 4, only examined as part of the UWTV survey.

Site	1970	1980/81	1991	1992	1993
2. Main Channel				0.024	0.060
1. South Cumbraes		0.268		0.034	0.073
5. Loch Fyne				0.077	0.077
3. South of Arran	0.9–1.4		1.388	0.127	0.265
4. South of Ailsa Craig			1.479	0.328	0.472
*South of Ailsa Craig			1.459		0.383
6. Holy Isle				0.045	0.064

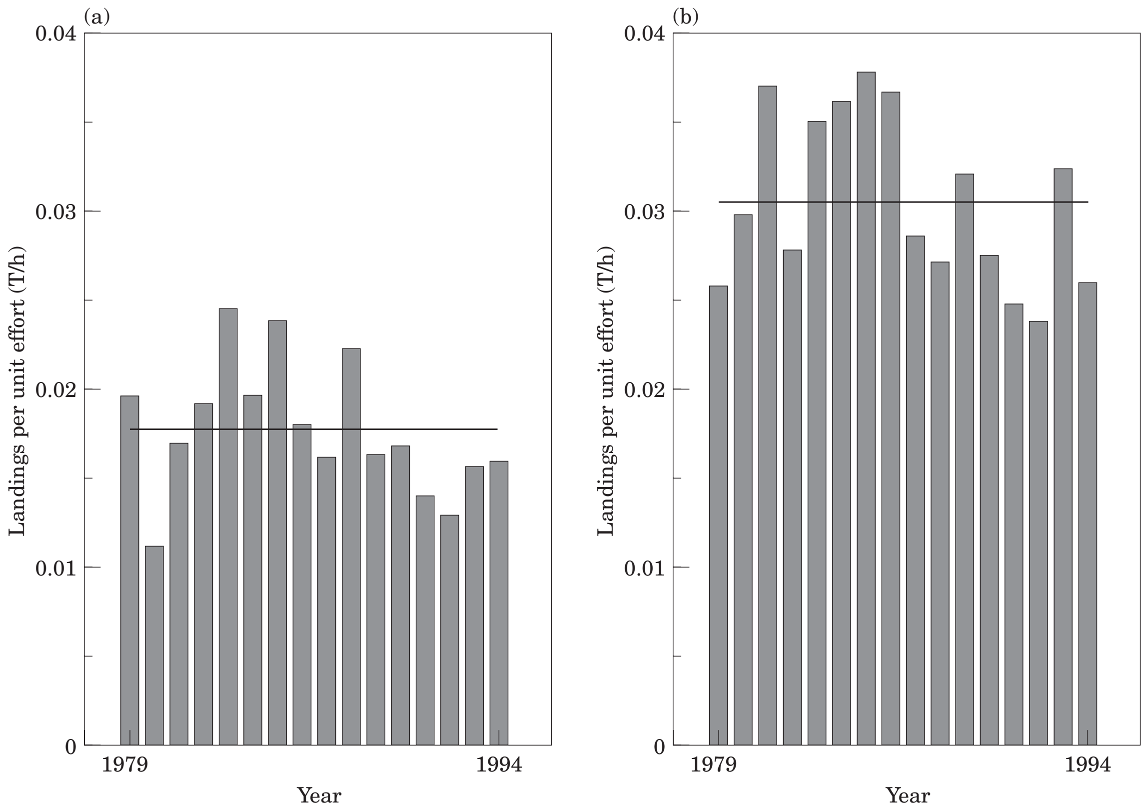

Figure 5. *Nephrops* single trawl landings per unit effort (mt h^{-1}) from 1979 to 1994 for: (a) Clyde Sea Area, and (b) Sound of Jura. Horizontal line represents the 16 year mean.

were approximately twice those reported for the CSA for the same period (1979–1994) (0.031 metric tonnes per hour (T h^{-1}) and 0.018 T h^{-1}, respectively) (Fig. 5a and b). Data for the CSA show that reported landings per unit effort since 1989 have consistently been below the 16 year mean, the lowest landings were in 1992. Landings in 1980 were the only instance of landings lower than in 1992. Figures for the Sound of Jura also show a reduction in landings after 1989, again with the lowest in 1992, but landings in 1993 recovered to above the 16 year mean.

Discussion

Transmission of *Hematodinium* infection in *Nephrops*

Comparisons of the length–frequency distribution of infected *Nephrops* at sites 1 and 4, show that medium-sized Norway lobsters of both sexes have the highest infection prevalences at those sites, and that more females than males are infected at each site, although the size at which the highest prevalences occur does not appear to vary with sex, as observed in earlier work (Field *et al*., 1992). Size/prevalence distributions in both males and females indicate that there may be a decrease in the maximum size at which the disease is found through the season. The mean size of *Nephrops* from populations of each of these two CSA regions is known to differ (northern populations being generally of larger animal size than southern ones due to differences in growth rate) (Tuck, 1993). It is therefore possible that the disease is expressed in particular age groups of individuals, these being of different sizes in populations where growth rates differ. Thus, expression of disease may be determined by the age of the host rather than by some factor directly related to size. The most likely predisposing factor is moulting.

Moult has already been implicated in the transmission of *Hematodinium* spp. infections in both *Nephrops* (Field *et al*., 1992) and *Chionoecetes bairdi* (Meyers *et al*., 1987, 1990), the *Nephrops* work suggesting that dinospores may enter new hosts through cuticular lesions directly after ecdysis. Smaller *Nephrops* moult more frequently than larger ones, and given that medium-sized lobsters and females within the CSA tend to moult in spring and early summer, it is possible that during moulting the animal is particularly sensitive to becoming infected, and thus, those animals moulting more frequently are more likely to be infected. Furthermore, Messick (1994) found that juvenile blue crabs (*Callinectes sapidus*) (which have thinner cuticles and moult more often than older crabs) exhibited higher prevalences of infection by *Hematodinium perezi* than did adult crabs.

In addition, the release of large numbers of dinospores from moribund host *Nephrops* has now been observed on a number of occasions during two disease seasons (Appleton, 1996). This spore release occurs at a time when many lobsters are moulting. This did not appear to be the case with Bitter Crab Disease in tanner crabs (*C. bairdi*), since parasite spore release occurred in late summer, whereas the majority of crabs moulted in spring (Meyers *et al*., 1990). The possibility remains, therefore, that spores may spend some time outside a host before infection, perhaps as an over-wintering hypnospore (Love *et al*., 1993).

Meyers *et al*. (1990) suggested an alternative hypothesis, that transmission is by vegetative haemolymph and/or tissue parasite stages, either by cannibalism or by release along with spores from moribund hosts. Our evidence tends to argue against this; when spore release occurs, it is generally from heavily infected hosts in which parasites are generally represented as spores (Appleton, 1996). The observations that infection prevalence was higher in postmoult *C. bairdi* (Meyers *et al*., 1990), and the implication that a similar situation pertains in *Nephrops* (Field *et al*., 1992), may not be directly indicative of the role of moult in the expression of disease, but of its role in the transmission process. *In vivo* growth data for *Hematodinium* sp. in *Nephrops* (Appleton, 1996) show that a period of several months elapses from the time that dinoflagellates are first detectable in the haemolymph (the sub-patent infection of Field and Appleton, 1996), to the appearance of clinical signs of heavy infection (patency). Furthermore, during this study, lobsters of all mount stages have been observed to harbour patent infection.

It is suggested that infection acquired after moulting in 1 year leads to patent disease and probably death in the next. Love *et al*. (1993) predict a development time of 15–18 months for *Hematodinium* sp. in tanner crabs (*C. bairdi*), supporting the assertion that disease is not developed within one season. The seasonal nature of *Hematodinium* sp. infection patency, supported by the results of the GLM, is a feature of most reported infections by *Hematodinium* spp. in crustaceans. This is likely to reflect the time taken for parasite numbers to increase to a level at which their presence becomes apparent. After transmission, a summer latency appears to occur within *Nephrops*. A long latency period is also apparent in infection of *C. bairdi* by *Hematodinium* sp. between bouts of patent disease (Love, 1992), probably because of the slow growth of parasites (Meyers *et al*., 1987). *Callinectes sapidus* also displays long periods of latency between seasonal episodes of patent *Hematodinium perezi* infection (Newman and Johnson, 1975).

Diel variation in *Hematodinium* prevalence

In *Nephrops*, the variation in emergence activity with light intensity has been well documented (see Chapman, 1980), and is also apparent in the present study. On the Clyde grounds surveyed, few animals were available to trawls at night, with highest catches in the morning (dawn and mid-morning), declining thereafter, which is fairly normal for the depth sampled (70 m). Another catch peak at dusk, often evident (Chapman, 1980), was seen only in the May samples.

Diel variation in *Hematodinium* prevalence was apparent in the data collected for males in samples taken March–May. For males, prevalence was found to be highest in midnight trawls (26.7%) and lowest in trawls from mid-morning and noon (13.6 and 7.7%, respectively) (Fig. 4a). This suggests that infected male *Nephrops* tend to be more available to the fishery and consequently out of their burrows during the night compared with uninfected *Nephrops*. The reasons for this are not clear; it could be due to a need to spend more time foraging, to impaired light/dark perception, disrupted burrowing behaviour, or other factors.

For females, whilst the highest disease prevalences were found in the midnight samples (similar to the data for the males), there was no significant diel variation in prevalence for females. Females show very different annual behaviour patterns compared with males, over-wintering within their burrows when ovigerous and emerging in the spring (Chapman, 1980), but the reason for the apparent diel behavioural difference between the sexes of infected *Nephrops* is unclear.

Fisheries implications of *Hematodinium* infection of *Nephrops*

The causative organism of Bitter Crab Disease (BCD) in Alaskan tanner crabs, which is responsible for serious economic and population losses (Meyers *et al*., 1987), shows many pathological and ultrastructural similarities to *Hematodinium* in *Nephrops* (Meyers *et al*., 1987; Field *et al*., 1992; Hudson and Shields, 1994; Field and Appleton, 1995). The drastic effects of *Hematodinium* infection on host populations, and therefore fisheries, apparent in BCD in Alaska (Meyers *et al*., 1987) have not been seen in *Nephrops*. However, the high *Hematodinium* prevalences within Scottish *Nephrops* populations have necessitated a consideration of fishery implications. There is now good evidence that all *Nephrops* showing patent *Hematodinium* infection (Field and Appleton, 1996) die within a matter of weeks after capture (Field *et al*., 1992, 1995) and that those captured with sub-patent (low-level) infection almost invariably develop patent disease and die (Appleton, 1996).

Burrow density counts, as assessed by underwater photography and/or UWTV survey, are an accepted indicator of stock density. The earliest such data from the CSA were obtained in 1970 (Chapman, 1979), but only one of the 1970 sites was visited subsequently (south of Arran) (see Table 6). Comparisons of 1970 and 1991 burrow density data for the South of Arran station show little difference, but in 1992 and 1993 burrow density was substantially lower. Similarly, 1980–1981 burrow densities South of the Cumbraes were an order of magnitude higher than in the 1992 survey. Burrow density was 0.268 m^{-2} (1 burrow in every 3.7 m^2 of sea bed), i.e. 8 × higher than was found in 1992. Burrow density South of the Cumbraes was higher in 1993, but still far short of 1980/1981 levels. For sites South of Arran, and south of Ailsa Craig, burrow density data exist for 1991. At the two sites where comparisons can be made, the 1991 densities were much higher (× 11 for South of Arran; × 4.5 for site south of Ailsa Craig) than those found in the 1992 survey. In the 1992 survey, some small burrows may have been overlooked South of Arran because of poor water clarity, but careful re-analysis of the videotape suggested that any under-estimate would have been small. The burrow density data for each of the sites for which comparative data exist for 1992 and 1993, indicate that 1993 densities were higher than those recorded in 1992 (exept at the Loch Fyne site), being up to twice as great in most cases.

The results presented here show the highest *Hematodinium* prevalences in the CSA in 1991 and 1992, with LPUE and burrow densities, both indicators of *Nephrops* abundance, showing a decrease around or after this time. There is no evidence of a direct causal relationship between these events within the data from the CSA, although there has been no increase in fishing effort within the Clyde over this period, which might account for a stock reduction. Whilst the observed putative decline in *Nephrops* abundance is probably not due solely to fishing pressure, ascribing it entirely to *Hematodinium* infection is also not warranted. However, the fact that during 1991–1992 a high proportion of trawled *Nephrops* showed patent *Hematodinium* infection, a condition that is almost certainly fatal, suggests that this disease should be considered as an important contributor to *Nephrops* mortality in these areas and a potential factor leading to a decline in LPUE. Furthermore, given the recent identification of similar levels of infection on Irish Sea grounds, the situation should be monitored closely.

Although elevated disease prevalence in night-trawled animals has been reported in this paper, trawling normally takes place in daylight, so reported prevalence levels should be internally consistent. There is some evidence from our work that infection might predispose *Nephrops* to capture by impairing movement and altering behaviour. Fishery mortality might therefore mask what would otherwise be disease-induced mortality. Further study of these aspects has commenced.

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