ICES Journal of Marine Science, 58: 814–823. 2001
doi:10.1006/jmsc.2001.1072, available online at http://www.idealibrary.com on IDEAL®

The relationship of *Hematodinium* infection prevalence in a Scottish *Nephrops norvegicus* population to season, moulting and sex

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Stentiford, G. D., Neil, D. M., and Atkinson, R. J. A. 2001. The relationship of *Hematodinium* infection prevalence in a Scottish *Nephrops norvegicus* population to season, moulting and sex. – ICES Journal of Marine Science, 58: 814–823.

The two major field methods (body colour and pleopod index) for the diagnosis of infection in the Norway lobster, *Nephrops norvegicus* by the dinoflagellate parasite *Hematodinium* were compared. Using the more reliable method, the pleopod index, which scores infection severity on a four-point scale, infection prevalence data were collected from a single fishing ground in the Clyde Sea area, western Scotland over a continuous period of 31 months. Peak infection prevalence occurs during the spring and is highest in small *N. norvegicus* [mean carapace length 28.1 (±0.67) mm in females and 30.9 (±0.50) mm in males] and in females. Mean infection severity increased from 1.05±0.03 during the low season (July–December) to 2.59±0.19 by the end of the main infection season (May), highlighting the progressive nature of patent infection over time. Infection prevalence is synchronous between the sexes in some seasons but not in others. Additionally, the proportion of recently moulted, infected males in the late season extends the duration of peak infection prevalence in certain years. Data from two adjacent fishing grounds in the Clyde Sea area also show that infection prevalence depends upon the population structure at a given site – the site with smaller animals showing the higher prevalence. An evaluation of methods for monitoring *Hematodinium* infection suggests that the pleopod method gives the most accurate estimation of prevalence in field-caught lobsters.

Keywords: *Hematodinium*, infection prevalence, parasite, moult cycle, *Nephrops norvegicus*.

Received 20 October 2000; accepted 27 April 2001; published electronically on 13 June 2001.

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Introduction

Populations of the Norway lobster (*Nephrops norvegicus*) provide one of the most valuable shellfish resources in the Northeast Atlantic, with annual landings in excess of 60 000 tonnes (Tuck *et al*., 1997). There is a major fishery for *N. norvegicus* in waters surrounding the United Kingdom, to which the Scottish fishery contributes over 76% (£57 million in 1999 – Fisheries Research Services, 2000, unpublished). The majority of the landings are from trawlers, with lobsters often having been "tailed" for sale as "scampi". Larger animals, captured by baited creels, are often exported live to continental Europe in specially designed "vivier" vehicles. The large fishery for *N. norvegicus* necessitates careful stock assessment and effort control (Tuck *et al*., 1997) and an important feature of such assessment is the estimation of natural (M) and fishing (F) mortalities. While fishing mortality is directly related to effort (E), little information is available on the rate of natural mortality in *N. norvegicus* populations (Chapman, 1980). Assessments of natural mortality in fisheries models should make use of available data on disease prevalence (Kuris and Lafferty, 1992).

Infections by parasitic dinoflagellates of the genus *Hematodinium* have been reported in a number of

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commercially important crustacean hosts (Newman and Johnson, 1975; Maclean and Ruddell, 1978; Messick, 1994; Meyers *et al*., 1987; Latrouite *et al*., 1988; Wilhelm and Boulo, 1988; Hudson and Shields, 1994; Hudson and Lester, 1994; Taylor and Khan, 1995; Wilhelm and Mialhe, 1996). Stocks of *N. norvegicus* on the West Coast of Scotland also harbour infections by *Hematodinium* (Field *et al*., 1992). Since the initial descriptions of disease etiology, diagnosis and pathology (Field *et al*., 1992; Field and Appleton, 1995, 1996), further studies have described the *in vitro* life-cycle of the parasite (Appleton and Vickerman, 1998) and have revealed that significant alterations in host physiology (Taylor *et al*., 1996), biochemistry (Stentiford *et al*., 1999; Stentiford *et al*., 2000a), locomotory performance (Stentiford *et al*., 2000b) and behaviour (Stentiford *et al.,* 2001a) are associated with parasitism. It is believed that patent infection leads to death, recovery of the host not having been observed to date.

A number of methods are available for the detection of *Hematodinium* infection in *N. norvegicus*. The simplest involves external assessment of the altered carapace colouration and opacity that accompanies patent infection. This assessment has the advantage that it can be performed rapidly in the field, but its value as a diagnostic tool has not been established, since no systematic study has been made of the relationship between parasite burden and colour change. The method that has been used most routinely is the pleopod infection staging technique of Field and Appleton (1995), in which a pleopod is assessed for the presence of parasites using low-power microscopy. This method assigns infection severity on a four-point scale, allowing the progression of infection to be charted. The first objective of the current study was to compare the sensitivity and reliability of the body colour and pleopod methods for the detection of patent infections.

Observations on the prevalence of *Hematodinium* infection in crabs have suggested that there is a highly seasonal epidemiology, with peak infection occurring over a relatively narrow time period, followed by a longer period of undetectable or low level infection prevalence (see Shields, 1994). Studies on *Hematodinium* infection in Scottish *N. norvegicus* populations have shown similar features of seasonal epidemiology, along with evidence that prevalence is higher in small lobsters than in large lobsters, and in female lobsters than in male lobsters (Field *et al*., 1992, 1998; Field and Appleton, 1995). Meyers *et al*. (1990) have reported that *Hematodinium* infection prevalence is highest in post-moult *Chionoecetes bairdi*. Moulting has also been suggested as the major predisposing factor for *Hematodinium* infection of *N. norvegicus*, though the relationship remains unclear (Field *et al*., 1992, 1998).

From a general survey of *Hematodinium* infection in *N. norvegicus* captured from the west coast of Scotland, it has been shown that the Clyde Sea area generally has the highest prevalence levels (Field *et al*., 1998). The second objective of the current study was therefore to investigate infection prevalence (using the pleopod method), over a prolonged period on a major *N. norvegicus* fishing ground in the Clyde Sea area. The data are discussed in relation to the importance of long-term *Hematodinium* infection monitoring in commercially important crustacean populations, and the requirement for accurate infection prevalence data for use in stock assessment models for the *N. norvegicus* fishery.

Materials and methods

Capture of lobsters

Norway lobsters (*Nephrops norvegicus*) were caught at a depth of approximately 80 m, using 90 min tows of a standard otter trawl (70-mm stretched mesh). The start of the towing period was always between 0900 h and 1000 h to minimise any effect of differential burrow emergence behaviour on catch composition (Atkinson and Naylor, 1976) and the effect of capture time on infection prevalence (Field *et al*., 1998). The main capture site was at a location immediately south of Little Cumbrae (LC) in the Clyde Sea area (55°41′N 4°56′W) or in one instance, from the adjacent Bute-Cumbrae channel (BC) (55°46′N 4°59′W) (see Figure 1). Both sites are commercially fished. Trawls were made each month over the period February 1998–August 2000 inclusive ($n=31$).

N. norvegicus were separated from bycatch on deck and a representative 5 kg sub-sample of lobsters was retained for the assessment of sex, carapace length, approximate moult stage and infection stage. Carapace length (mm) was measured from the rim of the eye socket to the posterior mid-point of the carapace. Moult stage was assigned as either intermoult (IM – no setal withdrawal in the pleopod and a rigid carapace) or recently moulted (RM – no setal withdrawal in the pleopod and a flexible "paper" carapace) (see Aiken, 1980). All sub-samples were stored in a cool, damp environment following capture and were generally alive for *Hematodinium* infection diagnosis by the pleopod method. Pleopods were viewed under low-power light microscopy (× 40 magnification). The accumulation of parasite material was used to assign the appropriate stage, whereby Stage 0 is apparently uninfected and Stages 1–4 are patently infected.

In a separate trial, the accuracy of the body colour and pleopod diagnosis methods was assessed by comparing the results from two different scorers (one naïve and one experienced). Both scorers assessed each lobster in a standard sub-sample for *Hematodinium* infection using the body colour method (loss of shell translucency, vivid colouration) and the pleopod method (as above).

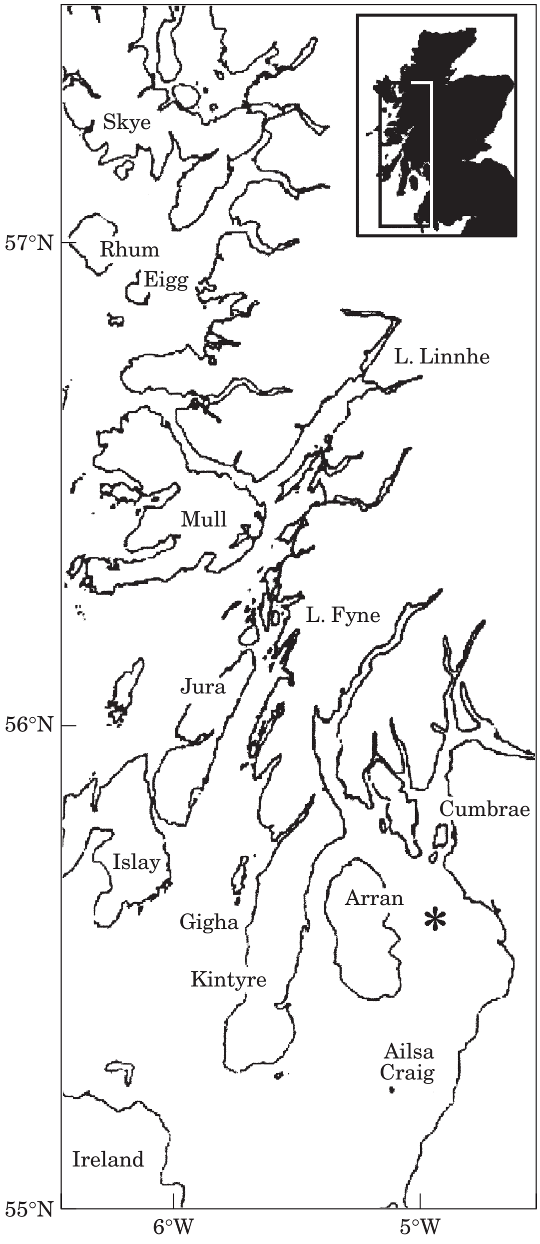

Figure 1. Map of western Scotland showing the sampling sites in the Firth of Clyde (asterisk). The University Marine Biological Station Millport (UMBSM) is situated on the Isle of Cumbrae in the Clyde estuary.

Results from the two scorers were compared at the end of the trial to assess the inter-operator sensitivity and reliability of the two methods.

Analysis of data

Comparisons of the mean size of infected male and female lobsters and the mean size of uninfected and infected lobsters from the LC and BC sites were performed either by one-way analysis of variance (ANOVA) for normally distributed data, or by a Mann–Whitney test for non-normal distributions. Tests were considered significant if p<0.05.

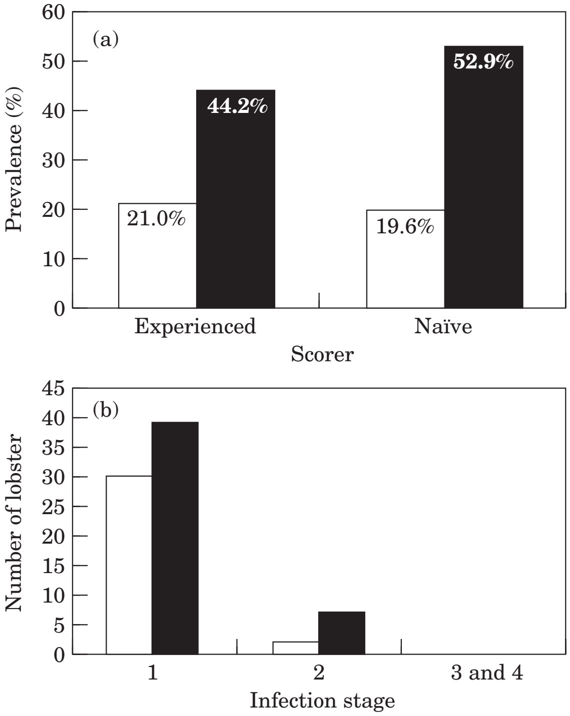

Figure 2. (a) Percentage *Hematodinium* infection prevalence detected using the body colour (open) and pleopod (filled) diagnostic methods by the naïve and experienced operators. (b) Number of lobsters diagnosed as infected by the pleopod method but not by the body colour method as a function of pleopod infection stage. Open bars represent experienced operators, filled bars represent naïve operators.

Results

Body colour vs. pleopod diagnosis

By comparing the scores of the experienced and naïve operators, it was possible to assess the sensitivity and reliability of the two major field diagnosis methods. Relative to the pleopod method, the body colour assessment underestimated infection prevalence by approximately 50%, even when used by the experienced operator [Figure 2(a)]. Of those infected lobsters misdiagnosed by the body colour method, the majority were assigned to Stage 1 infection by both scorers. However, no heavily infected lobsters were missed by the colour diagnosis method by either operator [Figure 2(b)]. The pleopod scores show that the naïve operator estimated infection prevalence to be approximately 9% higher than the experienced operator [Figure 2(a)]. Of these

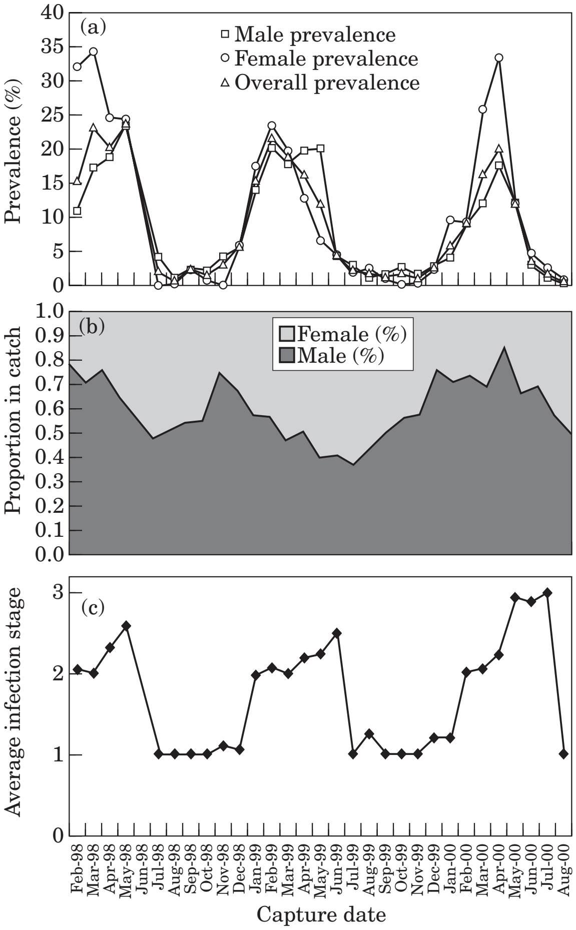

Figure 3. (a) Pleopod-derived *Hematodinium* infection prevalence, (b) proportion of males and females, and (c) average pleopod-derived infection stage, in monthly samples of *N. norvegicus* captured from the Little Cumbrae (LC) site between February 1998 and September 2000.

overestimates, the majority were lightly infected (Stage 1) animals.

Hematodinium prevalence at the LC site

Infection prevalence data obtained using the pleopod method at the LC site over three consecutive fishing seasons are shown in Figure 3(a). During the summer and autumn (July–November), the prevalence of patent infection was minimal in both male and female lobsters (<5%), with the initial increase occurring during December in each of the seasons studied. Prevalence of patent infection showed a marked increase during the period between January and March, and peaked in April or May. Overall infection prevalence reached a maximum of 20–25% in each of the three seasons studied, though prevalence in female lobsters was as high as 35% during the 1998 and 2000 seasons. However, the elevated level of infection prevalence in female lobsters had a lesser effect on the overall infection prevalence, due to the reduced proportion of female lobsters in the catch during the late winter and early spring periods [Figure 3(b)]. Following the peak (May–July), there was a sharp reduction in the prevalence of patently infected lobsters.

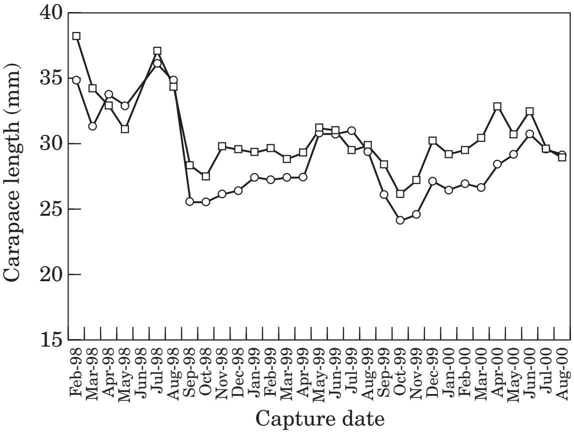

Figure 4. Mean carapace length of monthly samples of *N. norvegicus* captured from the Little Cumbrae (LC) site between February 1998 and September 2000. —○—, female; —□—, male.

Severity of patent *Hematodinium* infection

As well as allowing *Hematodinium* infection prevalence to be assessed at the population level, the pleopod staging method also allows an assessment of the severity of infection (on a four-point scale). The mean infection severity measured in lobsters displaying patent infection, captured at the LC site over the three consecutive seasons, is shown in Figure 3(c). Over this period, all *Hematodinium* infected lobsters captured during the "low season", i.e. outwith the main infection season of July–December, had very low parasite burdens, with a mean infection stage of 1.05 ± 0.03 (n = 12). At the beginning of the main infection periods (February), the mean severity of infection in infected lobsters increased significantly to 2.04 ± 0.02 (n = 3), and then to 2.59 ± 0.19 (n = 3) (heavy *Hematodinium* burden) by the end of the main infection season (May). These data indicate a progressive nature of patent infection over the main infection period.

Size of infected lobsters

The monthly data for mean carapace size of lobsters captured at the LC site are given in Figure 4. In addition to a reduction in mean carapace lengths, which occurred during the autumn (September–October) of each season studied, the mean carapace length of male lobsters was significantly smaller in the 1999 season [29.2

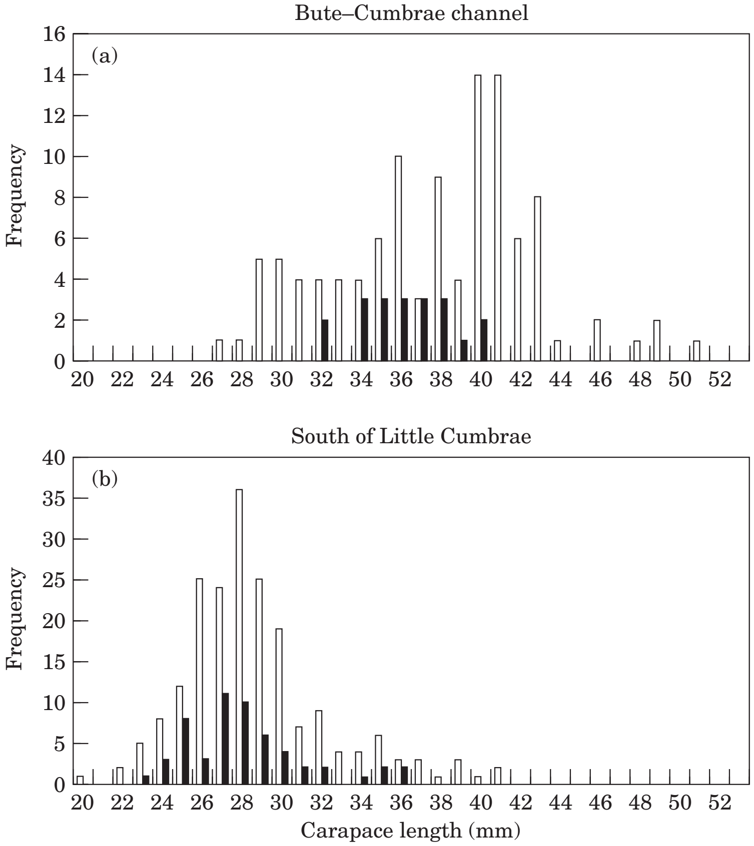

Figure 5. Carapace length frequency distributions for the Bute-Cumbrae channel (a) and Little Cumbrae (b) sites. Uninfected lobsters are shown as open bars and infected lobsters as filled bars.

(± 0.4) mm] than in the 1998 season [32.3 (± 1.15) mm]. However, no significant reduction in carapace length was seen in females over the same period [30.7 (± 1.4) mm in 1998; 27.8 (± 0.7) mm in 1999]. In the 2000 season, the mean sizes of male and female lobsters [30.7 (± 0.5) mm and 28.2 (± 0.6) mm, respectively] were not significantly different to those in the 1998 season.

The mean carapace length of *Hematodinium*-infected female lobsters [28.1 (± 0.67) mm] was significantly smaller than that of infected male lobsters [30.9 (± 0.50) mm] captured from the LC site. In order to test whether the mean carapace length of the *N. norvegicus* population at a particular site affects the prevalence of *Hematodinium* infection in that population, two adjacent sites (LC and BC) were sampled on the same day in February 1999. Overall infection prevalence at the BC site was 15.5%, while at the LC site, prevalence was 21.6%. The mean carapace length of uninfected lobsters captured at the BC site [37.5 (± 0.47) mm] was significantly greater than those at the LC site [28.6 (± 0.26) mm]. Similarly, the mean carapace length of *Hematodinium*-infected lobsters captured at the BC site [36.2 (± 0.52) mm] was significantly greater than those from the LC site [28.1 (± 0.42) mm]. At both sites the mean carapace lengths of uninfected and infected lobsters were not significantly different [Figure 5(a) and (b)].

Hematodinium infection and the moulting period

The relative proportion of recently moulted (RM) and intermoult (IM) *N. norvegicus* in the catch gives an indication of the main moulting period and allows an assessment of the synchrony of moulting amongst individuals in the population. Moult data from the LC site are shown in Figure 6(a). Large numbers of RM lobsters appeared in the catch during the spring and summer of each year, but the relative proportion of RM lobsters appeared to vary between seasons (with a particularly high proportion of RM females during the summer of 1998). The reduction in the proportion of RM lobsters in the catch during late summer seems to be due to the progression of moulted lobsters into the IM state as the season advances. The fact that there is a higher proportion of RM female lobsters than RM male

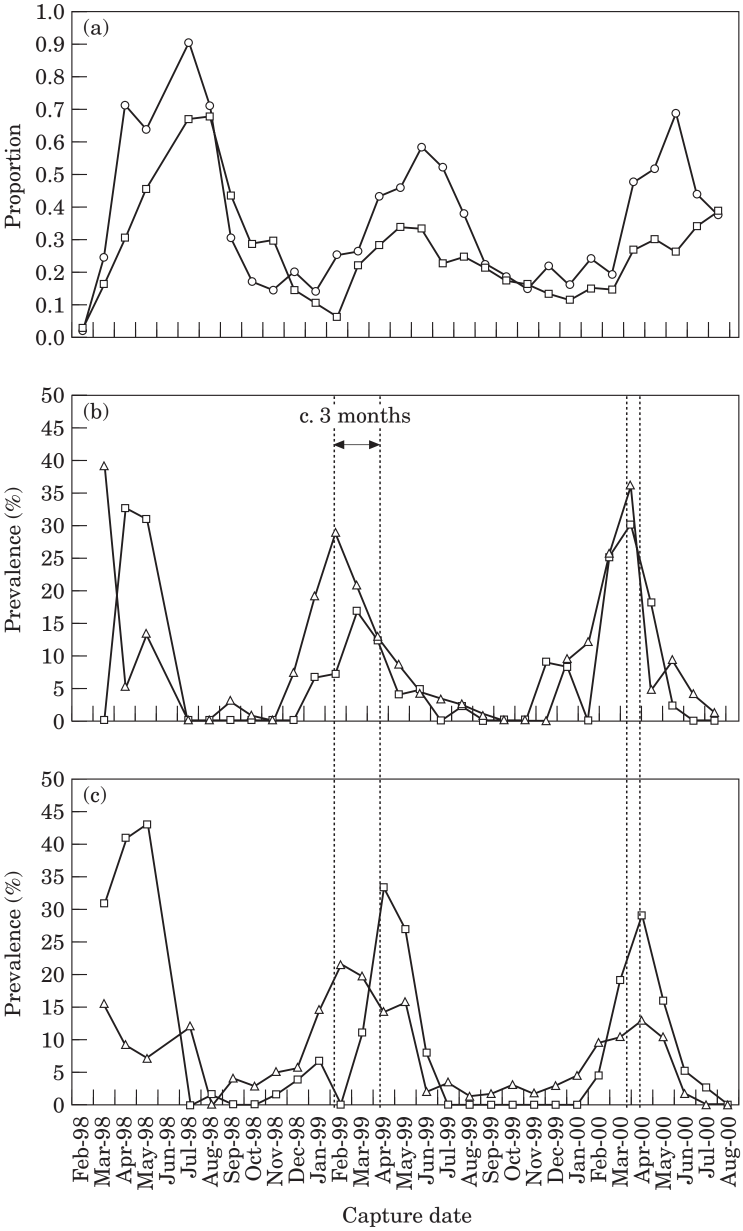

Figure 6. (a) Proportions of recently moulted (RM) and intermoult (IM) male (—□—) and female (—○—) *N. norvegicus*. Infection prevalence in RM (—□—) and IM (—△—) (b) female and (c) male lobsters at the Little Cumbrae site between March 1998 and September 2000. Broken lines on Figures (b) and (c) compare RM and IM infection prevalence seasons in female and male lobsters (see main text).

lobsters each spring and summer is suggestive of a more synchronous moulting period in females than in males, even though RM lobsters of both sexes are found in the catch throughout the year.

By combining data for moult status and infection prevalence and comparing the prevalence level in RM and IM lobsters, it is possible to investigate the relationship between moulting and the onset of disease patency in each sex. Figure 6(b) shows infection prevalence data for RM and IM female lobsters at the LC site. In the 1998 season, prevalence was initially high in IM female lobsters, and increased in RM female lobsters as the season progressed. In the 1999 season, IM prevalence also rose initially, though the prevalence level in RM females did not increase to the level seen in the 1998 season. In the 2000 season, the prevalence level in IM and RM female lobsters was similar for the whole season. In contrast, male lobsters displayed a similar pattern of IM and RM infection prevalence for each of the seasons studied [Figure 6(c)], with RM infection prevalence being consistently higher than IM infection in the late season (April–May).

In some seasons (e.g. 1999), data for overall infection prevalence at the LC site [Figure 3(a)] show an apparent "plateau" of peak infection prevalence between February and April–May. When data from the 1999 season for RM and IM female lobsters are compared to those of RM and IM male lobsters, it can be seen that infection prevalence peaks later in males than in females and that the plateau of infection prevalence described above is caused by an increase in infection prevalence in RM males [Figures 3(a) and 6(c)]. During other seasons (e.g. 2000), male and female infection prevalence peaks coincide causing a sharper peak of infection prevalence [see broken lines between Figure 6(b) and (c)].

Discussion

The body colour vs. pleopod diagnostic methods

The body colour diagnostic method uses external features of infection (vivid colouration, opaque carapace) to estimate prevalence. It is rapid and can be carried out aboard research and fishing vessels. However, the current study has shown that it may underestimate infection prevalence relative to that determined by the pleopod method, by approximately 50%. No improvement in diagnostic accuracy occurred with experience, both the naïve and experienced operators failing to diagnose large numbers of early-stage (Stage 1) infections. This suggests that while this method may be useful for the selection of heavily infected lobsters from the catch for pathological studies, the colour changes in lobsters with light infections are too minor to be used for accurate diagnosis. As such, the body colour method probably has little use in providing accurate data for modelling the proportion of natural mortality (M) attributable to *Hematodinium* infection (Field *et al.*, 1992).

The pleopod diagnosis method detected considerably more infected lobsters than the body colour method, but the higher prevalence estimate made by the naïve operator suggests some subjectivity in this method, especially for the diagnosis of light infections. As the pleopod method determines the presence of *Hematodinium* parasites in the haemolymph, any other changes to the haemolymph following capture are likely to affect diagnostic accuracy. In the hours following capture, colonisation of the haemolymph by bacteria was often observed, making visual assessment of light infections more difficult. Sample freshness is therefore important, especially for the diagnosis of light infections. Overall, however, the pleopod diagnostic method provides a reliable, rapid and relatively transferable tool for infection assessment and is therefore useful for preliminary studies in *N. norvegicus* fisheries where the presence of *Hematodinium* infection is unconfirmed.

Hematodinium infection epidemiology

The pleopod diagnostic method has been used to highlight the seasonal, epidemic nature of *Hematodinium* infection in a population of *N. norvegicus* contributing to the important commercial fishery in the Clyde Sea area. This reinforces earlier reports of a high prevalence of *Hematodinium* at other sites on the west coast of Scotland (Field *et al.*, 1992, 1998). During the study period, three discrete seasonal episodes of *Hematodinium* infection occurred (each spring), in which overall prevalence reached 20–25%. Previous data from the Clyde Sea area showed that peak infection prevalence can reach 70% in certain years (Field *et al.*, 1992), highlighting the potential for considerable variation in the absolute level of infection prevalence between years.

Infection prevalence was highest in female lobsters (especially during the 1998 and 2000 seasons). This may be attributed to the life history of female *N. norvegicus*, in which the egg-rearing period may last for up to eight months of the year, during which time the female remains, for the most part, within the burrow (Farmer, 1974a). Following spawning, the female emerges from the burrow (reflected by the increased proportion of female lobsters in the catch during late spring) to feed, moult and mate with a hard-shelled male (Farmer, 1974b). It has been proposed that mechanical disruption to the soft cuticle of the female lobster during copulation may lead to infection by motile spores of the *Hematodinium* parasite entering at the trauma site (Field *et al.*, 1992). However, although feasible, this would not explain transmission to male lobsters and such a route of transmission has not been demonstrated experimentally. It seems more likely that ingestion of parasites via suspension or filter feeding (Loo *et al.*, 1993), by predation of alternative hosts (e.g. hermit crabs) or by cannibalism are the most likely routes of transmission to and from *N. norvegicus*. Predation on amphipods which are also known to harbour *Hematodinium* infections (Johnson, 1986) is another possible transmission route.

The pleopod diagnosis method allows for an assessment of the absolute *Hematodinium* parasite burden in infected *N. norvegicus*. Field *et al.* (1992) showed that the majority of infected lobsters captured by trawling were in infection Stages 1 or 2.

However, the current study has shown that while mean infection severity in infected *N. norvegicus* is low during the summer months (mean approximately Stage 1), this increases as the infection season progresses (up to a mean of Stage 3). Increasing infection intensity through the main season is suggestive of a slow incubation of the parasite in the haemolymph, and reinforces previous data which showed that the *Hematodinium* parasite burden increased 100-fold over a period of 100 d in the haemolymph of aquarium-held infected lobsters (Appleton *et al*., 1997). The slow incubation of patent *Hematodinium* infection in the field may increase the chance of parasite transmission via cannibalism or predation, and occurs concomitantly with the progressive utilisation of host tissue and haemolymph storage products (Stentiford *et al*., 1999, 2000b).

Hematodinium infection and the moult cycle

An association between patent *Hematodinium* infection and moulting has been described by a number of workers, though due to the inherent complexities of the moulting process, the details of this relationship remain unclear (Meyers *et al*., 1987; Field *et al*., 1992, 1998; Messick, 1994). By assessment of shell condition, the current study has shown that in some years, the extended infection season is caused by high infection prevalence in RM male lobsters during the late season (April–May). In other years, where infection prevalence rises and falls more abruptly, prevalence in RM and IM males and RM and IM females coincides, creating a sharper infection peak. It is probable that in seasons of very high peak infection prevalence (>70%), the infection prevalence in male and female lobsters peak at the same time. Therefore, in terms of absolute natural mortality (M) attributable to *Hematodinium* infection, the length of the infection season may be as important as the absolute peak prevalence level.

During the final stages of the pre-moult and in the post-moult periods, storage material is mobilised (from tissue to haemolymph) to sustain the animal over the non-feeding stages of the life cycle (Johnson, 1980; Icely and Nott, 1992). This mobilisation may create haemolymph conditions which are conducive to proliferation of the parasite population (see Stentiford *et al*., 2001b). Female crustaceans have relatively larger amounts of hepatopancreatic tissue than males (Farmer, 1974b) and the higher incidence of *Hematodinium* infection in female lobsters may reflect some relative advantage of the female host to the parasite. This benefit may be enhanced in smaller lobsters, which contain relatively larger amounts of hepatopancreatic material per unit size, store larger amounts of reserve material for moulting (Heath and Barnes, 1970), and in the case of males (and immature females), moult more frequently than larger lobsters (Sarda, 1995; González-Gurriarán *et al*., 1998).

Hematodinium infection and the fishery for *N. norvegicus*

Our data suggest that the mean carapace length of lobsters has reduced at the LC site in the Clyde Sea area over the past three years. A reduction in the mean carapace length of the *N. norvegicus* population on a particular fishing ground is one symptom of stock over-exploitation (Sarda, 1998). However, this reduction may also be due to high recruitment at the same site over the same period (Marrs *et al*., 2000). The significant difference in mean carapace length between the BC and LC sites also suggests that the population structure of *N. norvegicus* differs between sites. Field *et al*. (1998) showed that the mean carapace lengths of *Hematodinium* infected *N. norvegicus* may differ between sites, but they did not compare the mean size of these infected animals to that of the whole catch. The current study has shown that the mean size of infected lobsters was not significantly different to that of the whole sub-sample at either the LC or BC sites. However, the overall prevalence at the two sites was different, suggesting that population structure may play a part in the overall *Hematodinium* infection prevalence. There may be strong moulting synchrony amongst individual lobsters in populations of small, size-matched, rapidly growing individuals. As described above, populations with such characteristics may experience the highest *Hematodinium* infection prevalence. Further investigations on the effect of carapace size distributions on infection prevalence should be carried out to determine the importance of fishing pressure in the generation of population structures suitable for *Hematodinium* epidemics to occur.

Due to the severe pathological effects associated with advanced *Hematodinium* infections, the survival of infected lobsters under aquarium conditions (Field *et al*., 1992; Field and Appleton, 1995) and the sporulation response which leads to the death of the host lobster (Appleton and Vickerman, 1998), it is unlikely that lobsters recover from patent infection. Seasons of high infection prevalence have been associated with reductions in landing per unit effort (lpue) and burrow density (Field *et al*., 1998). Accurate prevalence estimates should allow a *Hematodinium* infection mortality factor (M_H) to be incorporated into natural mortality (M), with this factor being greater during seasons where infection prevalence is highest. Previous attempts to incorporate the high observed prevalence of *Hematodinium* infection into analytical stock assessments of the Clyde Sea area modelled the effect as an additional loading on the natural mortality rate M (since animals showing symptoms of patent infection usually die) (ICES, 1997). However, the exercise was not entirely successful because it led to unrealistic estimates of recruits entering the fishery.

The accuracy of infection prevalence estimates from trawl caught *N. norvegicus* samples has been questioned, due to the severely reduced escape swimming capacity (Stentiford *et al*., 2000b) and the increased out-of-burrow activity (Stentiford *et al*., 2001a) of infected lobsters. Increased catchability of infected lobsters relative to their uninfected counterparts may lead to considerable overestimation of true prevalence on a particular fishing ground. If infected animals are more susceptible to predation through a reduced ability to escape, then the infection may not necessarily add to overall natural mortality, but rather replace a proportion of it. In addition, any increased catchability of infected lobsters may increase fishing mortality. The altered catchability of patently infected lobsters and the subjectivity in detecting light infections raise doubts about the accuracy of the pleopod method for estimating *Hematodinium* infection prevalence from trawl-caught samples, and about the usefulness of these data for estimating natural mortality due to *Hematodinium* infection. Development of sensitive molecular methods for the non-subjective detection of latent and subpatently infected lobsters, which are less likely to show behavioural changes due to parasitism, should allow these issues to be resolved.

Acknowledgements

This work was supported by a contract from the Ministry of Agriculture Fisheries & Food of the United Kingdom (Contract No. CSA 4172, Project code MFO221). The authors wish to thank Mr Mick Parker and the crew of the RV "Aora" (University Marine Biological Station Millport) for assistance in the collection and sorting of animals and Mr Mats Ulmestrand (Institute of Marine Research, Sweden) and Ms Susanne Tarnlund (University of Gothenburg, Sweden) for participating in inter-operator scoring comparisons.

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