DIURNAL ACTIVITY IN A GROUP OF GULF OF MAINE DECAPODS

BY

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ABSTRACT

The patterns of diel activity of four large decapod species in the shallow subtidal of the Isles of Shoals, Gulf of Maine, U.S.A. were investigated. During the summer of 1999 the diel abundance and size distribution of active decapod individuals were surveyed at three depth ranges at a sheltered site on Appledore Island. Densities of active American lobsters, *Homarus americanus* H. Milne Edwards, 1837, were, as expected, highest at night. The crabs *Cancer borealis* Stimpson, 1859 and *Carcinus maenas* (L., 1758), however, were almost exclusively active during the day. *Cancer irroratus* Say, 1817 were equally active during the day and the night, but the mean size of individuals was significantly larger during the day. Surveys at additional sites in 2003 confirmed that these same patterns of diel activity were present throughout the Isles of Shoals. An extensive review of the literature suggests that such diurnal activity is not only unusual for the three crab species of this study, but for the whole genus *Cancer* as well.

ZUSAMMENFASSUNG

Untersucht wurden die Muster der Tag-Nacht-Aktivität vierer großer Dekapoden-Arten aus dem Flachwasser der Isles of Shoals im Golf von Maine, U.S.A. Auf der geschützten westlichen Seite der Insel Appledore sind im Sommer 1999 Individuenzahl und Größenverteilung aktiver Dekapoden in drei Tiefenbereichen ermittelt worden. Der Amerikanische Hummer *Homarus americanus* H. Milne Edwards, 1837 erwies sich erwartungsgemäß als nachtaktiv, während die beiden Krabben *Cancer borealis* Stimpson, 1859 und *Carcinus maenas* (L., 1758) fast ausschließlich tagaktiv waren. *Cancer irroratus* Say, 1817 war tags genauso aktiv wie nachts, bloß war die durchschnittliche Körpergröße der Individuen am Tage signifikant größer. Stichproben im Bereich dreier weiterer Inseln im Jahr 2003 zeigten, dass diese Arten im Gesamtbereich der Isles of Shoals dieselben Muster der Tag-Nacht-Aktivität aufweisen. Eine umfassende Literaturrecherche ergab, dass die hier festgestellte Tag-Nacht-Aktivität nicht nur für die drei untersuchten Krabben höchst ungewöhnlich ist, sondern auch für alle Arten der Gattung *Cancer* insgesamt.

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INTRODUCTION

Many organisms exhibit distinct diel patterns of activity, either for the avoidance of predators or competitors (Flecker, 1992; Jones et al., 2001), due to prey availability (Zemke-White et al., 2002) or physiological tolerances (Walsberg, 2000), or because of their phylogenetic history (Learner et al., 1990). Diel activity, in marine decapods in particular, is generally considered to be nocturnal (Warner, 1977; Dunham, 1983; Webb, 1983; Naylor, 1988). A large body of literature specifically regarding four Gulf of Maine decapods describes the American lobster, *Homarus americanus* H. Milne Edwards, 1837, the Jonah crab, *Cancer borealis* Stimpson, 1859, the rock crab, *Cancer irroratus* Say, 1817, and the green crab, *Carcinus maenas* (L., 1758) as nocturnal foragers that retreat to shelter during diurnal periods of inactivity (see Discussion). However, observations beginning in 1998 at the Isles of Shoals suggested that local crab populations were more active during the day than the night (pers. obs.).

In the Gulf of Maine, *H. americanus*, *C. borealis*, *C. irroratus*, and *C. maenas* constitute a dominant and abundant group of large, highly mobile animals that have both ecological and commercial significance. In the shallow subtidal, densities of adult and subadult decapod populations are highest during the summer months (Ennis, 1984a; Witman, 1985; Ojeda & Dearborn, 1990) in rocky habitats (Fogarty, 1976; Hudon & Lamarche, 1989; Stehlik et al., 1991) where they are preyed upon by fishes (Ojeda & Dearborn, 1991; Witman & Sebens, 1992) and seabirds (Dumas, 1990; Good, 1992). Showing a high degree of habitat-specific overlap in their opportunistic diets of bivalves, gastropods, and echinoderms (Ennis, 1973; Elner & Campbell, 1987; Ropes, 1989; Stehlik, 1993), the four species not only share the same shelter and prey resources, but also exploit these in similar ways. Crabs, however, are also an important component of the lobster diet (Hudon & Lamarche, 1989; Ojeda & Dearborn, 1991; Sainte-Marie & Chabot, 2002).

The observation of unusual diel activity patterns within this group was thus of interest not only in regard to the prevailing literature, but from an ecological perspective as well. This study presents confirmation of diurnal activity in the crab assemblage at Appledore Island in 1999 and throughout the Isles of Shoals in 2003. Day and night-time surveys of active individuals showed that while *H. americanus* were primarily active at night, *C. borealis* and *C. maenas* were primarily diurnal; *C. irroratus* were equally active during the day and the night. An extensive review of the literature suggests that such diurnal activity is not only unusual for the three crab species of this study, but for the whole genus *Cancer* as well.

MATERIALS AND METHODS

Study area

The Isles of Shoals (42°58′N 70°37′W) form an archipelago of nine islands situated approximately 10 km off the coasts of Maine and New Hampshire in the southern Gulf of Maine (fig. 1). The western sides of the islands, sheltered from the prevailing eastern and south-eastern summer swells, typically consist of sloping bedrock that extends to depths of approximately 15 m below Mean Lower Low Water and are dominated by macroalgae (*Chondrus crispus* (L.) J. Stackhouse, coralline turf, *Codium fragile* (Suringar) Hariot, and a number of *Polysiphonia*-like species). Isolated clumps of horse mussels (*Modiolus modiolus* (L., 1758))

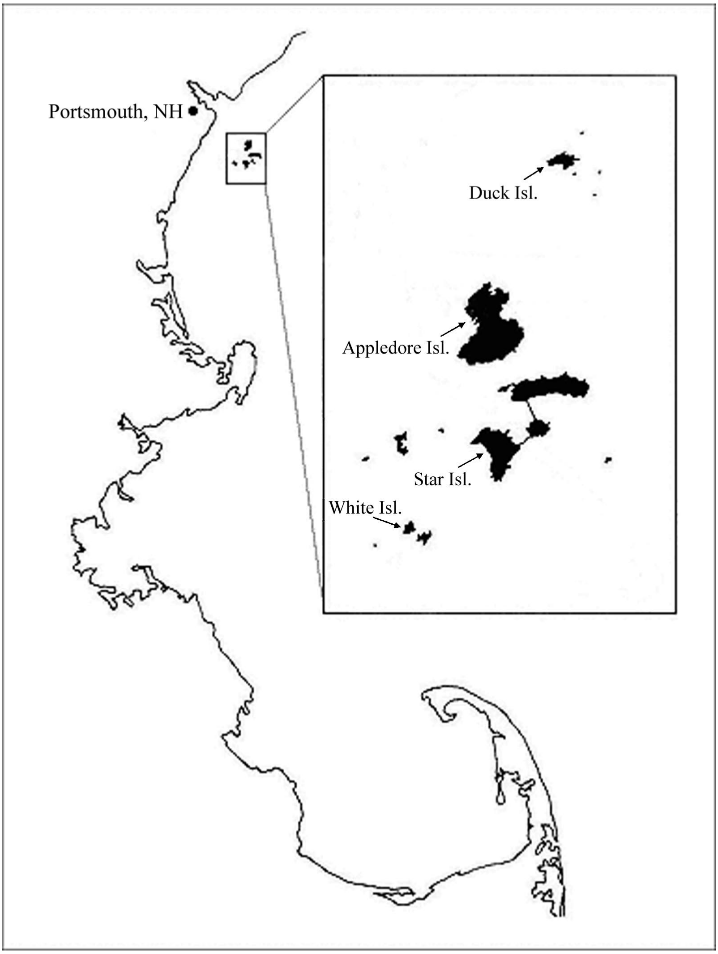

Fig. 1. Map of the southern Gulf of Maine showing the location of study sites among the Isles of Shoals (inset).

and shotgun kelp (*Agarum clathratum* (Dumortier)) are often found among the rock rubble that occurs at 13-15 m depth where the substrate changes to sand.

Patterns of diel activity and depth distribution — Appledore Island 1999

To investigate the variation in the depth distribution and the size structure of the four decapod species over their diel cycles of activity, day- and night-time surveys were conducted in a 200 m stretch of the west side of Appledore Island (fig. 1) between June and August 1999. Using SCUBA, each survey consisted of counting and measuring all active individuals (those not buried or in crevice shelters) in three 20×1 m band transects haphazardly placed parallel to the shore within each of three depth ranges (1-3 m, 5-7 m, and 9-11 m below water surface level). Five day and three night-time surveys were conducted although, in total, 69 transects were made, as three night-time 9-11 m transects could not be completed. Night-time censuses were conducted using lights covered by red cellophane to reduce startling effects in the decapods (Kennedy & Bruno, 1961). Active individuals were counted and measured to the nearest cm (carapace width (CW) for crabs, carapace length (CL) for lobsters).

After transforming densities $[\sqrt{(\text{density} + 1/2)}]$ to reduce heteroscedasticity, a two-way ANOVA was used to examine the effects of depth and time (day vs. night) on the density of each of the four decapods. Comparing the effects of these factors on the size distribution of the decapods using a two-way ANOVA was not possible due to the absence of individuals at certain combinations of time and depth. A one-way ANOVA on transformed sizes ($\sqrt{\text{CW}}$ or $\sqrt{\text{CL}}$) was therefore used to test for differences between means for each species, with either time or depth as the independent variable. Scheffe's (1953) F procedure of unplanned a posteriori contrasts (SC) was used to compare densities and sizes between the depth ranges following a significant ANOVA. All analyses were performed in StatView 5.0.1.

Patterns of diel activity — Isles of Shoals 2003

Similar surveys to those of 1999 were repeated in July and August of 2003 to assess whether or not the patterns observed on Appledore Island were representative of decapod activity patterns throughout the Isles of Shoals. Three additional sites of similar aspect, substrate, and algal cover were selected on three islands: Duck, Star, and White (fig. 1). Each of the four sites was surveyed twice for the abundance and size distribution of active decapods, once during the day and once at night, by performing three 20×1 m transects haphazardly placed parallel to the shore at depths between 3 and 9 m (below water surface level). At each site, day- and night-time surveys were conducted between 10 and 12 hours apart to ensure similar tidal levels; daytime surveys were thus conducted between 9 and 11 a.m. and night-time surveys between 9 and 11 p.m.

After transforming densities [$\sqrt{(\text{density} + ½)}$], a two-way ANOVA was used to examine the effects of site and time (day vs. night) on the density of each species. To test for differences in the mean size of individuals during the day versus the night the data of all four sites were pooled and a one-way ANOVA on square-root transformed sizes was used for each species.

Literature review

The ISI Web of Science (Science Citation Index Expanded, 1945-Aug. 2003) was used with the topic keywords "*Cancer* AND crab", "*Homarus americanus*", and "*Carcinus maenas*" to perform a review of publications mentioning the diel activity of any of the four species and the whole genus *Cancer*. The full text of all ecological publications was read to discern whether accounts of diurnal or nocturnal activity in the species were of an anecdotal nature, whether laboratory trials using the species had been conducted under light or dark conditions, or whether formal comparisons of day and night-time activity had been conducted, either in the field or in the laboratory. Accounts of larval behaviour were not included in the review.

RESULTS

Patterns of diel activity and depth distribution — Appledore Island 1999

The four species exhibited three general patterns of diel activity (fig. 2). Active *Homarus americanus* were ten times more abundant during the night than the day (day mean density ± SE = 0.02 m^{-2} ± 0.00, night mean density ± SE = 0.20 m^{-2} ± 0.03, $p < 0.0001$). Active *Cancer borealis* and *Carcinus maenas* were, respectively, eleven and seven times more abundant during the day than at night (*C. borealis*: day 0.11 m^{-2} ± 0.02, night 0.01 m^{-2} ± 0.00, $p < 0.0001$; *C. maenas*: day 0.07 m^{-2} ± 0.03, night 0.01 m^{-2} ± 0.01, $p = 0.007$). Active *Cancer irroratus*, however, did not exhibit any significant diel difference in density (day 0.14 m^{-2} ± 0.03, night 0.12 m^{-2} ± 0.02, $p = 0.85$).

C. borealis ($p = 0.050$) and *C. maenas* ($p = 0.024$) densities exhibited significant depth by time-period interactions. During the day, active *C. borealis* densities at 9-11 m were greater than at 1-3 m (SC, $p = 0.034$) and 5-7 m (SC, $p = 0.020$). During the day, active *C. maenas* densities at 1-3 m were greater than those at 5-7 m (SC, $p = 0.0001$) and 9-11 m (SC, $p < 0.0001$).

H. americanus ($p = 0.86$), *C. borealis* ($p = 0.28$), and *C. maenas* ($p = 0.78$) showed no significant differences between day- and night-time sizes of active individuals (fig. 3a). Diurnally active *C. irroratus* individuals, however, were significantly larger than nocturnal individuals (mean difference ± SE = 0.65 cm

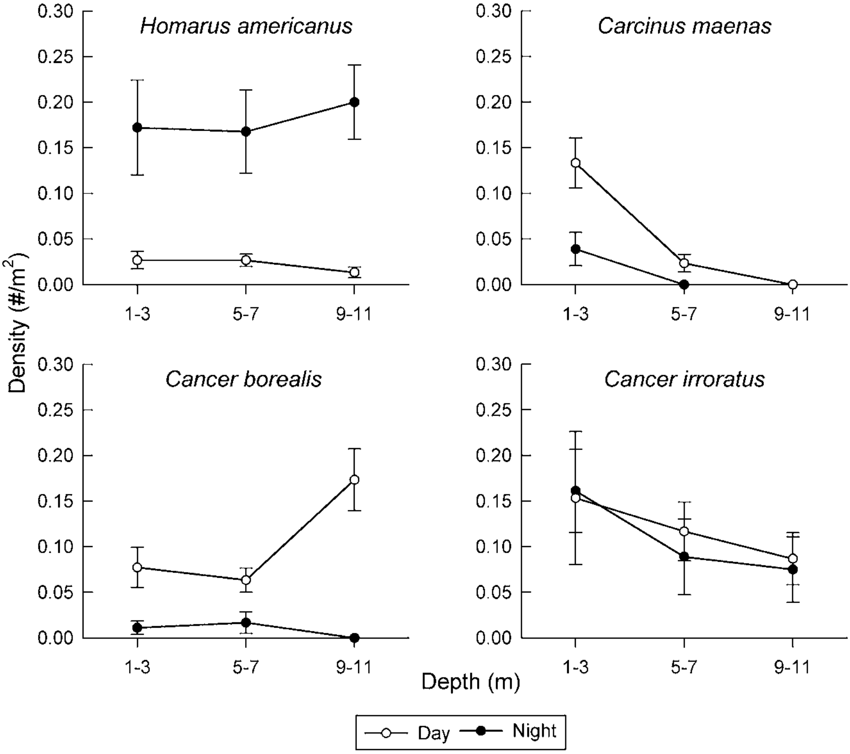

Fig. 2. Diel depth distributions expressed as the mean density (±1 SE) of active *Homarus americanus* H. Milne Edwards, 1837, *Cancer borealis* Stimpson, 1859, *Cancer irroratus* Say, 1817, and *Carcinus maenas* (L., 1758) individuals in surveys conducted on the western side of Appledore Island in 1999.

± 0.30, $p = 0.006$). Diurnal *C. borealis* were larger at 9-11 m than at 1-3 m (2.1 cm ± 0.7, SC, $p = 0.002$), and diurnal *C. maenas* were larger at 5-7 m than at 1-3 m (1.4 cm ± 0.8, SC, $p = 0.030$).

Patterns of diel activity — Isles of Shoals 2003

The same patterns of activity that were observed on Appledore in 1999 were observed on Appledore Island and the three additional sites in 2003 (fig. 4). Active *H. americanus* were six times more abundant during the night than the day (day mean density ± SE = 0.03 m^{-2} ± 0.02, night mean density ± SE = 0.17 m^{-2} ± 0.05, $p = 0.009$) and active *C. borealis* were twenty times more abundant during the day than the night (day 0.35 m^{-2} ± 0.05, night 0.02 m^{-2} ± 0.01, $p < 0.0001$). *C. maenas* were four times more abundant during the day than the night, but this difference was not significant (day 0.08 m^{-2} ± 0.0, night 0.02 m^{-2} ± 0.01, $p = 0.077$). Active *C. irroratus* did not exhibit significant diel differences in density (day 0.64 m^{-2} ± 0.19, night 0.68 m^{-2} ± 0.20, $p = 0.60$).

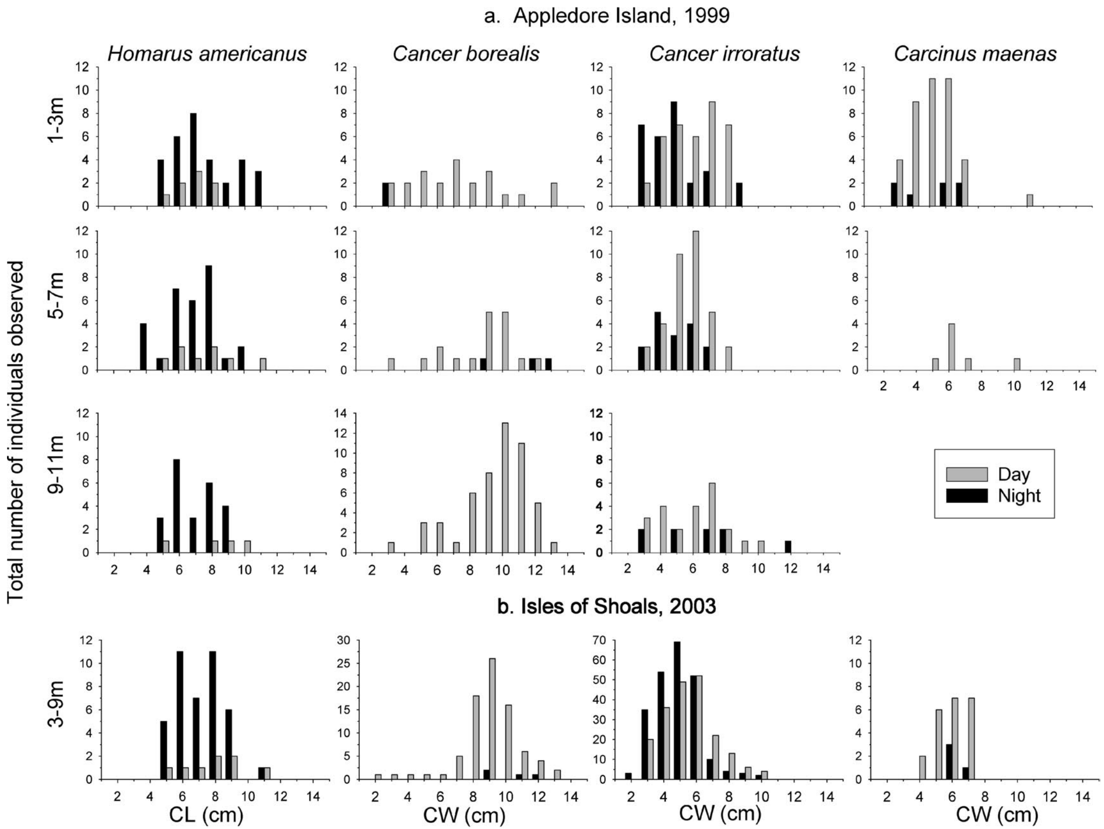

Fig. 3. Size-frequency distributions of active *Homarus americanus* H. Milne Edwards, 1837, *Cancer borealis* Stimpson, 1859, *Cancer irroratus* Say, 1817, and *Carcinus maenas* (L., 1758) individuals in day- and night-time surveys conducted on: a, Appledore Island in 1999; and, b, four sites throughout the Isles of Shoals in 2003.

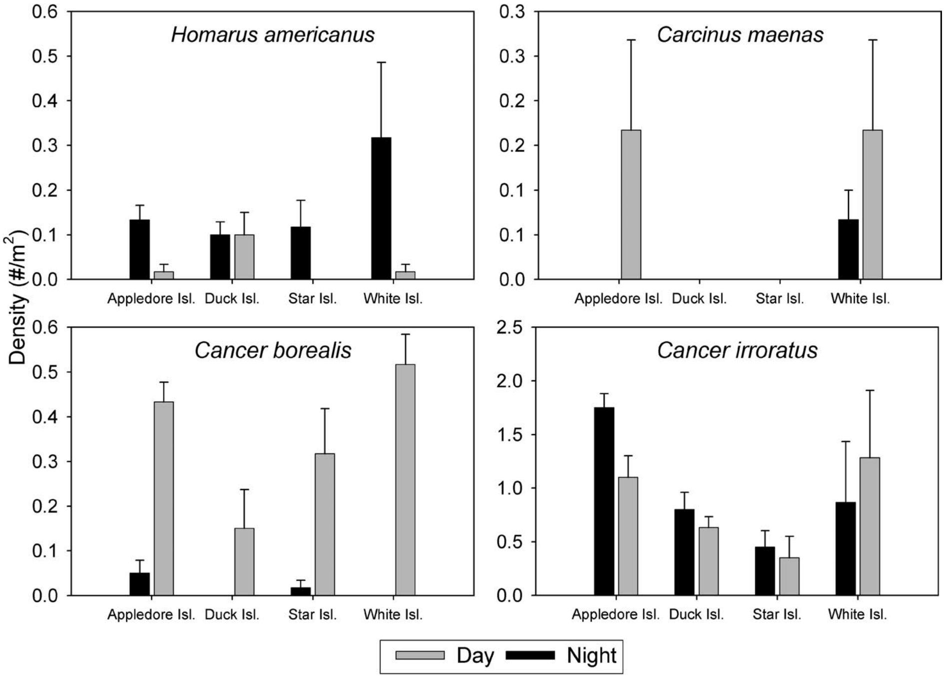

Fig. 4. Diel mean density (±1 SE) of active *Homarus americanus* H. Milne Edwards, 1837, *Cancer borealis* Stimpson, 1859, *Cancer irroratus* Say, 1817, and *Carcinus maenas* (L., 1758) individuals in surveys conducted at four sites throughout the Isles of Shoals in 2003.

The four sites differed significantly in the densities of active *C. borealis* ($p = 0.019$) and *C. irroratus* ($p = 0.028$), but not of active *H. americanus* ($p = 0.47$) (fig. 4). No *C. maenas* were counted in surveys conducted at Duck and Star Island, but a site effect was not significant ($p = 0.077$). *C. borealis* densities exhibited a significant site by time-period interaction as no active individuals were observed at Duck and White Island during the night ($p = 0.037$).

Pooled across all sites, the mean sizes of active *H. americanus* ($p = 0.20$), *C. borealis* ($p = 0.22$), and *C. maenas* ($p = 0.52$) did not differ significantly between the day and the night (fig. 3b). Diurnally active *C. irroratus* individuals, however, were significantly larger than nocturnal individuals (mean difference ± SE = 0.7 cm ± 0.1, $p < 0.0001$).

Literature review

Ninety-one of the publications that were returned by the keywords mentioned diel activity patterns for one or more of the four Gulf of Maine species. (In laboratory-based studies this was most often done in reference to the condition of light or darkness under which trials had been conducted.) Explicit comparisons of day- and night-time activity levels were performed in only 45 (49%) of these

TABLE I

Summary of publications in which the day- and night-time activity levels of the four Gulf of Maine decapods and crabs of the genus *Cancer* were explicitly compared; anecdotal observations and publications regarding larval behaviour were not included

	Diurnal	Nocturnal	No diel difference
Homarus americanus H. Milne Edwards, 1837	–	9, 13-17, 20, 21, 22, 25, 30, 39, 41, 50	26, 60
Carcinus maenas (L., 1758)	–	1-5, 23, 27, 29, 34, 36-38, 44, 46, 48, 51, 53, 56, 62	10, 11, 33, 58
Cancer borealis Stimpson, 1859	–	8, 16, 20, 22, 30, 31	–
Cancer irroratus Say, 1817	39, 45	8, 16, 19, 20, 24, 31, 39	57, 63
Cancer spp.	48	6, 7, 12, 18, 28, 32, 35, 40, 42, 47-49, 52, 59, 61	43, 54, 55

[1]Naylor, 1958; [2]Kitching et al., 1959; [3]Naylor, 1960; [4]Crothers, 1967; [5]Ropes, 1968; [6]Ansell, 1973; [7]McDonald et al., 1973; [8]Fogarty, 1976; [9]Zeitlinhale & Sastry, 1978; [10]Aldrich, 1979; [11]Depledge, 1978; [12]Gotshall, 1978; [13]Reynolds & Casterlin, 1979; [14]Pottle & Elner, 1982; [15]Ennis, 1983; [16]Richards et al., 1983; [17]Ennis, 1984b; [18]Stevens et al., 1984; [19]Rebach, 1985; [20]Witman, 1985; [21]Lawton, 1987; [22]Ojeda, 1987; [23]Rangeley & Thomas, 1987; [24]Rebach, 1987; [25]Karnofsky et al., 1989; [26]Karnofsky & Price, 1989; [27]Reid & Naylor, 1989; [28]Robles et al., 1989; [29]Aagaard et al., 1991; [30]Ojeda & Dearborn, 1991; [31]Stehlik et al., 1991; [32]Wolff & Cerada, 1992; [33]Hunter & Naylor, 1993; [34]Burrows et al., 1994; [35]Chatterton & Williams, 1994; [36]Aagaard et al., 1995a, [37]1995b; [38]Aagaard, 1996; [39]Barbeau et al., 1996; [40]Karlsson & Christiansen, 1996; [41]Miller & Rodger, 1996; [42]Naylor et al., 1997; [43]Ramsay et al., 1997; [44]Zeng & Naylor, 1997; [45]Barbeau et al., 1998; [46]Gibson et al., 1998; [47]McGaw & McMahon, 1998; [48]Nickell & Sayer, 1998; [49]Skajaa et al., 1998; [50]Spanier et al., 1998; [51]Ansell et al., 1999; [52]Boulding et al., 1999; [53]Burrows et al., 1999; [54]Melo, 1999; [55]Smith et al., 1999; [56]Styrishave et al., 1999; [57]Zhou & Rebach, 1999; [58]Grosholz et al., 2000; [59]Smith et al., 2000; [60]Jury et al., 2001; [61]McDonald et al., 2001; [62]Wennhage, 2002; [63]Wong & Barbeau, 2003.

publications (table I). These publications included 22 comparisons performed in the laboratory, and 23 in the field.

The genus *Cancer* comprises 23 extant species at present (Hines, 1991). To complement the publications concerning *C. borealis* and *C. irroratus*, however, 31 publications were found mentioning the diel activity of one or more of only 9 further species: *C. pagurus* (L., 1758) (12), *C. magister* (Dana, 1852) (7), *C. productus* (Randall, 1839) (5), *C. oregonensis* (Dana, 1852) (3), *C. polyodon* (Poeppig, 1836) (2), *C. setosis* (Molina, 1782) (2), *C. bellianus* (Johnson, 1861) (1), *C. gracilis* (Dana, 1852) (1), and *C. novaezelandiae* (Jacquinot, 1853) (1). Eighteen (58%) of these studies performed explicit comparisons of day and night-time activity levels (table I). Details pertaining to the day and night-time activity patterns of all the species included in the review are considered below.

DISCUSSION

In this study, *Homarus americanus* were mostly restricted to nocturnal periods of activity, an observation in accordance with all but two previous publications (table I): these two studies suggest that, given a sufficiently strong bait stimulus, the catchability of lobsters in traps can be equal during the day and the night (Karnofsky & Price, 1989; Jury et al., 2001). Lobsters exhibit an intimate association with their shelters (Cobb, 1971). Lawton (1987) observed diurnal emergence from shelters in the laboratory only among subdominant lobsters in the presence of larger individuals or after periods of starvation. In this study, 13% and 20% of all active lobsters (in 1999 and 2003, respectively) were observed at daytime. However, mean lobster size did not differ between day and night-time periods suggesting that it were not simply subdominant individuals that were diurnally active.

In contrast to *H. americanus*, *Carcinus maenas* and *Cancer borealis* exhibited much higher densities of active individuals in the day than at night; *Cancer irroratus* did not show a diel difference in density, but the larger size of individuals during the day suggests that diel cycles of activity differed between segments of the population.

The literature suggests that such diurnal activity is highly unusual for the three crab species. *C. maenas*, which has been studied far more extensively than the two *Cancer* species, is described as being primarily nocturnal (table I). The species is known to exhibit strong circatidal patterns of activity (e.g., Reid & Naylor, 1989) thus some activity during daytime high tides is not unusual. On Appledore Island, for example, Hadlock (1980) noted that, "green crabs (*C. maenas*) were observed consuming individuals of *Littorina littorea* in tide pools at night and along the shore at high tide during the day". However, the overwhelming pattern found in previous studies has been one of higher activity levels during the night. Of the 22 studies of diel activity found for *C. maenas*, only two field surveys (Hunter & Naylor, 1993; Grosholz et al., 2000) and two laboratory comparisons (Depledge, 1978; Aldrich, 1979) failed to detect a difference in diel density or activity level. To my knowledge, no previous studies have documented higher day- than night-time activity as was observed in my surveys.

Six published reports of diel activity in *C. irroratus* and two anecdotal descriptions of its behaviour state that it, too, is a nocturnal species (table I). Only surveys performed by Barbeau et al. (1996, 1998) and a reference to unpublished video comparisons of day/night activity in the laboratory by Wong & Barbeau (2003) have shown that *C. irroratus* can exhibit similar levels of diurnal and nocturnal activity. In fact, the observations of Barbeau et al. (1996) suggest that diel activity may vary seasonally, such that *C. irroratus* are primarily diurnal in the summer and nocturnal in the winter. Unfortunately, all three publications cite either low crab numbers or generally low activity levels in such a way, that the strength of their inferences remains difficult to interpret.

In contrast to *C. maenas* and *C. irroratus*, the six studies on *C. borealis* have all described the species as predominantly active at night, both in field and in laboratory comparisons (table I). Two anecdotal accounts (Richards & Cobb, 1986; Richards, 1992) describe *C. borealis* as nocturnal as well.

Such diurnal activity appears to be quite unusual for the *Cancer* clade as a whole. Of the eight other *Cancer* species for which published comparisons were found, five have consistently shown higher nocturnal densities or activity levels. The three exceptions concerned the following species: (1) While the two field surveys of *C. productus* showed higher nocturnal activity (Robles et al., 1989; Boulding et al., 1999), a laboratory study showed low levels of night-time activity, not higher than those observed during the day (Smith et al., 1999). (2) A report on *C. bellianus*, a deep-water species, showed no diel differences in numbers captured in traps at depths of 200 to 700 m (Melo, 1999). (3) One of five diel studies of *C. pagurus*, the European edible crab, found no diel differences in the number of individuals attracted to fish discards (Ramsay et al., 1997). A second field study indicated higher diurnal densities in summer but higher nocturnal densities in winter (Nickel & Sayer, 1998).

Two explanations for the apparent uniqueness of the observations of diurnal crab activity at the Isles of Shoals are that (1) in contrast to populations elsewhere, activity patterns in local crab populations have changed such that diurnal activity is a recent phenomenon, or (2) local crab populations have always been diurnal (*C. borealis* and *C. maenas*) or partially diurnal (*C. irroratus*) but no one had previously examined diel activity patterns in the archipelago.

Only one previous publication has quantified diel densities in Isles of Shoals crab populations. Witman (1985) performed day and night surveys on the southern side of Star Island in 1982 and 1983 that differed from mine only in that (1) kelp and mussels dominated his site, whereas *Codium fragile* and *Polysiphonia* species dominated my sites, and that (2) he determined absolute decapod densities rather than counting only active crabs as I did. Witman (1985), however, found higher nocturnal densities of *C. borealis* and *C. irroratus*. (Witman (1985) makes no mention of *C. maenas*, for which the site may have been too exposed.) In conjunction with the anecdotal evidence provided by Hadlock (1980) for *C. maenas* on Appledore Island (see above), Witman's (1985) study thus suggests that explicit diurnal crab activity is a recent phenomenon in the Isles of Shoals.

Why such a change in activity patterns would have occurred only recently remains unclear. An explanation may ultimately lie in the loss of large predatory fishes at the Isles of Shoals in the early 1990s (J. B. Heiser, pers. comm.; Witman & Sebens, 1992). The overfishing of large predatory fishes such as cod (*Gadus* *morhua* (L., 1758)) and haddock (*Melanogrammus aeglefinus* (L., 1758)) has already been implicated in increased sea urchin and crab densities in coastal regions of the Gulf of Maine (Witman & Sebens, 1992; Vadas & Steneck, 1995) and may have released crabs from diurnal predation pressures. This may have increased the importance of crab interactions with nocturnally active lobsters and have indirectly resulted in increased diurnal crab activity: *H. americanus* preys upon and is dominant to the *Cancer* species in antagonistic interactions (Wang, 1982; Richards et al., 1983; Richards & Cobb, 1986).

What may be modifying this selection force of lobster-crab interactions, causing *C. irroratus* to exhibit a different pattern of diel activity than *C. borealis*, are the behavioural differences that exist between the two species. *C. irroratus* is a much more active species than is *C. borealis* (cf. Jeffries, 1966) and responds to confrontation by either fleeing or performing a stereotypical lateral merus display that involves the extension of its chelipeds and a raising of its body off the substrate. *C. borealis* does not flee, but rather crouches down, folding its appendages to cover its mouthparts and ventral surface (pers. obs.). Its behaviour may mean that *C. borealis* is more vulnerable to predation by *H. americanus* and that the selection force for diurnal activity may thus be stronger for this species than it is for *C. irroratus*. Supporting this hypothesis is evidence showing that the catchability of *C. irroratus* using lobster traps was not affected by the presence of *H. americanus* in the traps, while the number of *C. borealis* entering these traps was significantly reduced (Richards et al., 1983).

Though I am unaware of any study that has examined the interactions between *C. maenas* and the other three species, its smaller size suggests that it is an inferior competitor to *H. americanus* and the two *Cancer* species. I have also observed *H. americanus* preying upon *C. maenas* in the field (pers. obs.). The restriction of *C. maenas* activity to the shallowest depths during the day (where diurnal *C. borealis* are least abundant) may consequently be due to dual pressures of nocturnal and diurnal competition and predation. Similar diel separations of activity have been suggested in a number of communities in which species compete (e.g., Carothers & Jaksic, 1984; Kronfeld-Schor et al., 2001), and may be especially significant where additional predation occurs within the group (Polis et al., 1989), but this remains to be tested.

Regardless of the origin of the diurnal activity at the Isles of Shoals, the occurrence of crabs during the day has affected various interactions in the community. Most notably it appears to have strengthened the linkage between marine and terrestrial ecosystems by increasing the availability of crabs to predation by diurnally active gulls, *Larus argentatus* Pontoppidan, 1763 and *Larus marinus* L., 1758 which breed in the archipelago. In recent years, crabs (*C. borealis* in particular) have constituted up to 60% of the summer diet of these species (Rome & Ellis, in press). At the Isles of Shoals, changes such as these underline the importance of understanding the ecological history of the region and need to be incorporated into future studies of community and ecosystem dynamics.

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