

Abstract.—Eight female cunners, *Tautoglabrus adspersus*, were tagged externally with ultrasonic transmitters in Newfoundland, and their activity pattern was recorded. They were active diurnally, commencing activity, on average, 55 minutes after sunrise and ceasing activity about 50 minutes after sunset. The diurnal activity period was interrupted by periods of inactivity usually lasting 5–15 minutes. Levels of activity varied daily and seasonally; seasonal changes were the most dramatic. On average, female cunners were active for more than 12.5 h/day in June–July and for only 3 h/day in October–November. Decrease in activity reflected decreasing day length; as photoperiod became shorter, cunners spent a much larger portion of the daylight period inactive (22.9% in June–July compared with 71.8% in October–November). Decrease in cunner activity in the fall occurred while water temperature was as high as that in June and July and is speculated to be controlled by an endogenous rhythm.

Daily and seasonal activity patterns of female cunner, *Tautoglabrus adspersus* (Labridae), in Newfoundland

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Cunner, *Tautoglabrus adspersus*, is the most northerly distributed labrid fish in the western North Atlantic, reaching the northern extent of its range in waters off Newfoundland. A member of a large, essentially tropical, family, it is well known for its annual state of prolonged physiological torpor, which in Newfoundland may last for more than 6 months (Green and Farwell, 1971). The ability of cunners to undergo a long period of torpor is apparently one of the factors that have enabled this species to flourish in a low temperature environment (Curran, 1992). In waters off Newfoundland, cunners are abundant and inhabit sites where summer maximum water temperature is less than 11°C and the winter minimum is below -1°C. Newfoundland cunners enter and remain in torpor when seawater temperature is below about 5°C (Green and Farwell, 1971).

Throughout their range, Chesapeake Bay to the Strait of Belle Isle, cunners are associated with inshore habitats that provide shelter during nocturnal quiescence (a characteristic of labrids) as well as during

overwintering torpor (Pottle and Green, 1979a). Rather than migrating to deeper, warmer water as the temperature declines in the fall, Newfoundland cunners take shelter under boulders and rocks at their summer feeding and reproductive sites. There they remain until the seawater temperature approaches 5°C the following year, usually in early June (Green and Farwell, 1971). In Conception Bay, Newfoundland, territorial males establish territories within a week of emerging from winter torpor and maintain them until just prior to reentering winter torpor, usually in late November or early December (Pottle and Green, 1979a). Spawning commences in mid to late July, depending upon water temperature, and lasts for 2–3 weeks. All spawning activity occurs within male territories (Pottle and Green, 1979b; Martel and Green, 1987).

We recently reported on a home-range size for adult female cunners in Conception Bay, Newfoundland, that was based on telemetry data

from fish tagged with ultrasonic transmitters (Bradbury et al., 1995). Female cunners occupy small home ranges (300–2,353 m²) and exhibit seasonal variation in the size of their home range. The largest home ranges occur during June and July, a time when cunners are replacing energy stores depleted during winter torpor (Bradbury et al., 1995). This is also the time of year with the longest photoperiod and hence with the maximum potential foraging period for a diurnal species.

In this study, we report on the daily activity patterns of the female cunners in Conception Bay. Cunners at the northern extent of their range are of interest because their prolonged winter torpor may reduce annual foraging time. We expected that as the photoperiod decreased, female cunners would be active for more of the diurnal period, both to maximize growth and increase energy stores in preparation for six months of winter torpor.

Methods

Tracking

A fixed hydrophone array tracking system (Bradbury et al., 1995) was used to monitor the activity of eight female cunners tagged with ultrasonic transmitters in Broad Cove, Conception Bay. The system provided positional information (fixes) on a tagged fish once every 15 seconds. The change in the quality of the transmitter signal when a tagged cunner sought shelter by going under a boulder or into a crevice between two rocks enabled us to monitor activity-inactivity patterns accurately in much the same way as Chapman et al. (1975) had done with Norway lobster (*Nephrops norvegicus*). For a description of the tracking system, tagging procedure, and study site see Bradbury et al. (1995). With our tagging procedure, a tag holder and dummy tag were initially attached to fish in the field. After a week (minimum period), a fish with a tag holder and dummy tag was recaptured by a diver, and the dummy transmitter was replaced with a functional one. The latter procedure involved handling the fish for 1–2 min, from capture to release.

Tagged cunners were from 194 to 250 mm in total length (Table 1). At this size female cunners in Conception Bay are sexually mature (Pottle and Green, 1979a). Fish were tracked from June until November, i.e. during most of the period between the end and start of winter torpor. Lightning damage to the tracking system limited the amount of tracking that could be done in August. Individual fish were tracked for 4 to 32 days during which they all remained in the area encompassed by the hydrophone array. For

Table 1

Total length and tracking dates for female cunner tagged with ultrasonic transmitters in Broad Cove, Conception Bay, Newfoundland.

Fish identification	Total length (mm)	Tracking dates	Track duration (days)
A	194	17 Jun–30 Jun 5 Jul–6 Jul	14 2
B	215	18 Jun–4 Jul	17
C	250	28 Jun–21 Jul	24
D	235	12 Jul–21 Jul	10
E	195	15 Aug–18 Aug	4
F	225	30 Aug–22 Sep	16
G	245	23 Sep–20 Oct	22
H	240	21 Oct–24 Nov	32

the duration of the tracking period, information on water temperature, sea state, tidal phase, and cloud cover was available on a daily basis, as described by Bradbury et al. (1995).

Activity-inactivity

A tagged cunner was determined to be active or inactive based on information from the tracking system. If a strong transmitter signal was received, and positional information was obtained, the subject was considered active. If, on the other hand, signals were weak and no positional fix could be determined for more than 3 min (12 possible fixes), the fish was considered inactive. With scuba or snorkel equipment, divers documented over a period of >20 h that cunners had retreated into cracks and crevices or underneath objects when transmitter reception was poor. These observations also showed that female cunners do not “rest” on the substrate in open sites.

During the night, cunners seek shelter and undergo a period of nocturnal quiescence during which positional fixes cannot be obtained. The first and last positional fixes of the day therefore marked the beginning and end of diurnal activity. Onset of diurnal activity was expressed as the number of minutes before or after sunrise, whereas cessation of diurnal activity was expressed as the number of minutes before or after sunset. The duration of diurnal activity for an individual was defined as the total elapsed time between the onset and cessation of its daily activity.

Cunners also entered shelter (became inactive) at various times throughout the day; sites where cunners were inactive are termed day-rest sites. The duration of each inactive period (the time between

the initiation and the end of a poor transmitter signal) was recorded. On the basis of these data, the portion of the diurnal activity period spent inactive was calculated and expressed as a percentage.

In describing the activity-inactivity patterns of female cunners, five parameters were used: 1) onset of activity, 2) cessation of activity, 3) duration of diurnal activity, 4) length of inactivity bouts, and 5) percent of diurnal activity period spent inactive.

Analysis of data

Although a fish was handled for only 1–2 min when a transmitter was inserted into its tag holder and although field observations did not detect any changes in the behavior of fish following this procedure, nonparametric paired *t*-tests were used to examine whether female cunners showed similar activity on the first complete day of tracking (day 2) compared with the following day of tracking (day 3). All five activity parameters were tested.

A nonparametric analysis (Wilcoxon matched-pairs signed-ranks test) was used to compare inter-individual differences in activity between the two pairs of subjects tracked during the same periods (Table 1). Comparisons were made between fish A and fish B for a total of 11 days (i.e. June 18, 19, 20, 21, 22, 24, 25, 27, 28, 29, and 30) and between fish C and fish D for a total of 9 days (i.e. July 13–21 inclusive) for all five activity parameters.

A least-squares multiple regression analysis was used to determine whether date, time of day (i.e. morning vs. afternoon), or environmental variables (water temperature, cloud cover, and sea state) had a significant effect on activity. All activity parameters were tested. Because the activity data were normally distributed, no transformations were carried out. Although there were 141 tracking days, some days could not be used for certain activity parameters. For example, there were only 72 tracking days during which both the time of onset and cessation of activity were known for any given fish, both of which are required to calculate the duration of diurnal activity.

The tidal cycle was divided into four phases: low-tide, flood-tide, high-tide, and ebb-tide as described by Bradbury et al. (1995). For fish A, B, C, and D, mean activity parameters (i.e. percentage of time spent inactive and length of inactivity bouts) were determined for each tidal phase for the duration of the tracking period. An analysis of variance with three factors was used to test for intra- and inter-individual differences in activity during the tidal phases. We included only the fish by tide interaction term in our analyses because we did not expect any temporal variation in tide (tide \times date) or activity

Table 2

Mean number of minutes before sunrise and after sunset when tracked female cunners began and ceased their diurnal activity. Because the data for onset of activity for fish E consisted of a single point, no standard deviation is given.

Fish identification	Onset (minutes before sunrise)			Cessation (minutes after sunset)		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
A	57.6	10.02	9	57.6	26.70	9
B	40.2	23.95	12	63.6	18.10	12
C	48.7	10.93	18	74.3	19.64	22
D	31.7	18.48	6	43.0	43.59	4
E	45.0	—	1	50.3	34.46	4
F	52.0	21.28	3	36.5	41.16	4
G	49.4	32.69	14	54.1	20.33	17
H	72.4	52.54	28	18.9	39.12	27
All	54.7	36.63	91	49.1	36.15	99

(fish \times date), given the relatively short time (i.e. 11 and 9 days) over which observations were made.

Paired comparison *t*-tests were used to examine whether the one female cunner tracked during both the prespawning and spawning period had the same activity patterns during both periods. All activity parameters were tested.

Statistical analyses were performed with Minitab (Minitab, Inc., 1992) or SPSSX (SPSS Inc., 1990) statistical software packages.

Results

There were no significant differences ($P > 0.05$, non-parametric paired *t*-test) in activity parameters between the first complete day of tracking (day 2) and the following day.

All tagged fish were active during the day, inactive at night. Activity commenced, on average, 55 minutes (SD=36.6) before sunrise and ceased 49 minutes (SD=36.2) after sunset; however, there was considerable daily variation among individuals (Table 2). Throughout the day, activity was interrupted by periods of inactivity, usually lasting 5–15 minutes. Among those fish tracked on the same day, there were no significant differences between subjects for any of the activity parameters (Table 3).

When water temperature was below 5°C, cunners were inactive. On 23 and 24 June, for example, strong northwesterly winds forced cold water into the study area causing the water temperature to drop from 6°C to 3°C and the cunners to be inactive for two days. On the morning of 26 June the water temperature

Table 3

Results of the Wilcoxon matched-pairs signed-ranks test (*t*-value) used to compare interindividual differences in activity between pairs of cunners tracked during the same periods (*n* represents the number of days during which comparisons were made). Critical values of *t* are derived from Rohlf and Sokal (1969). There were no significant differences between fish for any of the activity parameters tested.

Behavioral parameter	Comparisons between fish A and fish B			Comparison between fish C and fish D		
	<i>n</i>	<i>t</i> -value	Critical <i>t</i> -value (significance level)	<i>n</i>	<i>t</i> -value	Critical <i>t</i> -value (significance level)
Percent of time inactive	11	26	13 (0.0415) 14 (0.0508)	9	11	8 (0.0488) 9 (0.0645)
Length of inactivity bout	11	26	13 (0.0415) 14 (0.0508)	9	14	8 (0.0488) 9 (0.0645)
Onset of activity	9	15	8 (0.0488) 9 (0.0645)	7	6	3 (0.0391) 4 (0.0547)
Cessation of activity	8	10	5 (0.0391) 6 (0.0547)	7	5	3 (0.0391) 4 (0.0547)
Duration of diurnal activity	8	13	5 (0.0391) 6 (0.0547)	7	7	3 (0.0391) 4 (0.0547)

Table 4

Summary of multiple regression analysis on the effects of time of day (prior to 1200 h vs. after 1200 h), date, and environmental variables on activity of female cunner. A minimum of 62 days and a maximum of 89 days were incorporated in the regression analysis for the last three behavioral parameters. Percentage of variation accounted for by each variable is given. * = significant at 0.05 level; ** = significant at 0.01 level; and *** = significant at 0.001 level.

Behavioral parameter	<i>n</i>	Time of day	Date	Water temperature >5°C	Sea state	Cloud cover	Combined variables
Percent of time inactive	205	0.6	58.7***	0.2	0.3	0.1	59.9***
Length of inactivity bout	229	0.1	12.7***	2.8**	1.7*	0.2	17.5***
Onset of activity	75	NA	6.6*	1.9	0.0	0.1	8.6
Cessation of activity	83	NA	22.3***	0.2	0.0	0.5	23.0***
Duration of diurnal activity	62	NA	92.3***	0.9**	0.1	0.1	93.4***

again dropped to 3°C, resulting in cunners being inactive for the remainder of the day. Temperatures above 5°C had small but significant effects on length of inactivity bouts and duration of diurnal activity (Table 4). Length of bouts of inactivity tended to decrease with increasing water temperature, whereas the trend was reversed for the duration of diurnal activity. Water temperatures above 5°C had no significant effect on the onset or cessation of activity or on the percentage of time spent inactive.

Sea state had a significant ($P < 0.05$) effect on length of cunner inactivity bouts (Table 4), with bouts of inactivity tending to be longer on days with high surface waves. Sea state did not have a significant effect on other activity parameters. Cloud cover had no significant effect on any of the activity param-

eters. There was a trend, however, for females to remain inactive for longer periods (i.e. percentage of time spent inactive increased as well as length of inactivity bouts) as cloud cover increased. There was also a tendency for the duration of diurnal activity to decrease with increasing cloud cover. Neither percentage of diurnal activity period spent inactive or length of inactivity bouts differed between morning and afternoon (Table 4).

There was no significant difference in fish behavior owing to tides (Table 5), indicating that both fish A and fish B responded similarly to the tidal cycle. Furthermore, there was no significant difference in activity (i.e. percentage of time spent inactive) between the various tidal phases for fish A or fish B (Table 5). Finally, there were no significant differ-

Table 5

Results of analysis of variance performed on the percentage of time spent inactive by fish A and fish B during the four phases of the tidal cycle. df = degrees of freedom; SS = sum of squares; MS = mean of squares.

Source	df	SS	MS	F-value	Probability value P
Date	10	5,492.5	549.3	1.74	0.089
Fish	1	33.1	33.1	0.10	0.747
Tide	3	1,320.8	440.3	1.39	0.252
Fish × tide	3	771.5	257.2	0.81	0.490
Error	70	22,117.3	316.0		
Total	87	29,735.3			

ences between the tidal phases for the length of inactivity bouts of fish A and fish B ($F_{3,70}=1.57$, $P=0.204$; $F_{1,3}=0.4$, $P=0.756$), percent of time spent inactive by fish C and fish D ($F_{3,56}=0.50$, $P=0.685$; $F_{1,3}=0.79$, $P=0.505$) and length of inactivity bouts of fish C and fish D ($F_{3,56}=0.82$, $P=0.4986$; $F_{1,3}=1.94$, $P=0.134$).

Time of year, i.e. seasonal factors, accounted for 58.7% of the variation in the percentage of the diurnal activity period spent inactive, i.e. the amount of time spent in shelter between the commencement and cessation of daily activity (Table 4). Cunnners spent an increasing proportion of the diurnal period inactive from June through November. This factor accounted

for 12.7% of the variation in length of inactivity bouts (which increased over time as well) and for 6.6% and 22.3% of the variance in onset and cessation of activity, respectively (Table 4). The trend was for activity to begin later in the morning and to end earlier in the evening (in relation to sunrise and sunset) as the season progressed. Time of year accounted for 92.3% of the variation in duration of diurnal activity. As the seasons progressed and the photoperiod became progressively shorter, there was a corresponding decrease in the duration of diurnal activity (Fig. 1).

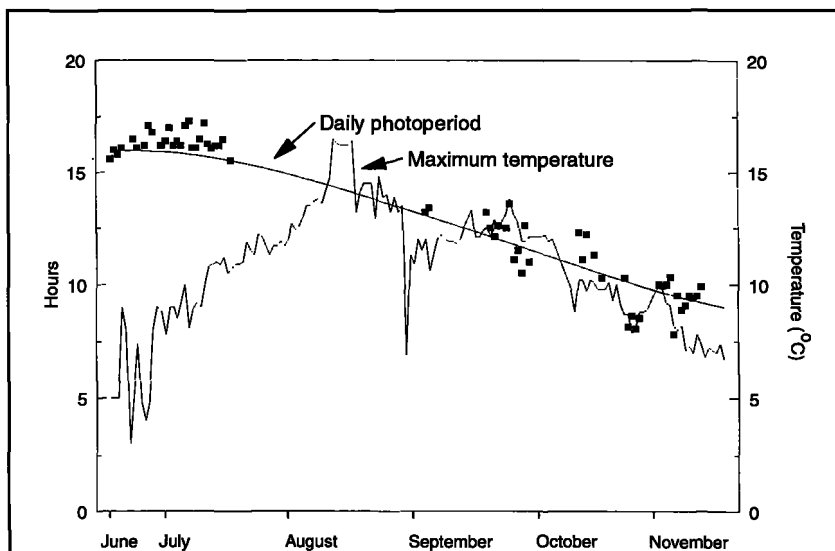
Thus the duration of cunner diurnal activity, percentage of time inactive, and length of inactivity bouts were all closely related to day length. By combining data from all subjects, the average elapsed time between onset and cessation of activity (i.e. duration of diurnal activity) was 16.5 h ($n=38$, $SE=0.10$) during June–July, 13.5 h ($n=8$, $SE=0.19$) during August–September, and 11.0 h ($n=27$, $SE=0.25$) during October–November. Cunner spent 22.9% ($n=35$, $SE=15.5$) of the diurnal period inactive between June and July, 47.0% ($n=13$, $SE=24.3$) of the diurnal period inactive in August–September, and 71.8% ($n=30$, $SE=13.2$) of the diurnal period inactive during October–November; length of inactivity bouts, on the other hand, increased from an average of 6.4 min ($n=64$, $SE=0.75$) in June–July to 9.3 min ($n=15$, $SE=1.56$) in August–September, to 12.7 min ($n=41$, $SE=1.14$) in October–November.

These data were used to calculate the number of hours a female cunner spent out of its shelter per day. On average, during June–July, female cunnners were active for 12.5 h/day, during August–September 7 h/day, and during October–November only 3 h/day. The remainder of the year was spent in winter torpor.

There were no significant differences ($P>0.05$, paired comparison t -test) in any of the activity parameters for the single female cunner tracked during both the prespawning and spawning periods.

Discussion

Pottle (1979) reported that in Newfoundland territorial male cunnners undergo periods of daylight quiescence under cover. Whoriskey (1983) also observed cunnners in Massachusetts underneath boulders at those times during the day when they were

**Figure 1**

Relation between length of daily photoperiod and duration of diurnal activity (■) for eight female cunnners tracked in Conception Bay, Newfoundland, between June 17 and November 24. Maximum daily seawater temperature at the study site is also shown.

not foraging. The female cunners we studied exhibited similar behavior, seeking shelter beneath rocks or in crevices during the day.

Some workers have assumed that temperate wrasses use cover to avoid predation (Olla et al., 1979; Hobson et al., 1981), although threat of predation has not been well documented as a factor. Whoriskey (1983) interpreted the diurnal use of shelter by cunners in Massachusetts as predator avoidance. Although he may have been correct, our field observations in Newfoundland do not support this hypothesis. Predation on adult cunners in Conception Bay is very low as judged by over 400 hours of diving observations during which no predation, or attempted predation, on adults was observed.

Females may seek shelter to avoid conspecifics with courting and chasing behaviors, especially territorial males. This explanation, however, is inadequate in elucidating why males exhibit the same behavior or why the behavior occurs so frequently outside the spawning period.

A reduction in energy expenditure may be associated with such behavior because cunners probably require less energy to maintain a position in a shelter than in the water column, even when water movement from currents and waves is minimal, and because the length of inactivity bouts increased with increased water turbulence. However, such an explanation is weak unless it can be shown that continued foraging would result in a net loss of energy.

In many diurnal fishes, including cunners, the onset and cessation of daily activity coincides closely with the rising and setting of the sun (e.g. Hobson, 1972, 1973; Hawkins et al., 1974; Olla et al., 1974, 1975; Clark and Green, 1990). As expected, females exhibited a marked seasonal decrease in the duration of their diurnal activity (from 16.5 h in June–July to 11.0 h in October–November) as day length decreased. Light intensity at sunrise and sunset was affected seasonally by the surrounding topography at the study site (e.g. in the fall the sun “set” behind a range of hills rather than at sea level), and this topography may have accounted for some of the seasonal change in the onset and cessation of diurnal activity. However, the considerable variation in the onset and cessation of daily activity among cunners suggests that this variation is not simply a response to a threshold light intensity.

Contrary to the expectation that female cunners would maximize foraging opportunities prior to entering winter torpor, they spent a larger percentage of the diurnal period inactive as the length of the photoperiod decreased. Why cunners should significantly reduce their foraging activity, at a time when food is still available and they could acquire more

energy for somatic growth and winter torpor, is not clear. Although water temperature is decreasing during this period, our analyses show that above $\sim 5^{\circ}\text{C}$, temperature has little direct effect in determining the ratio of activity to inactivity. Mean daily water temperatures during June–July and October–November were approximately the same (8.2°C and 9.2°C , respectively) (Fig. 1), yet there were large differences in the amount of time cunners spent in shelter. During June and July, females were outside their shelter for about 12.5 hours of the day, whereas from October to November cunners were active, on average, only 3 hours of the 11-h sunrise to sunset period.

Fall or winter decreases in the activity or feeding behavior (or both) of fishes in the absence of changes in water temperature are common, although the mechanisms underlying these decreases are not understood. Smith et al. (1993) for example found that in Atlantic salmon (*Salmo salar*), seasonal reductions in swimming activity and feeding were more closely related to day length and changes in day length than to other environmental variables, including water temperature. This also seems to be true for cunners. Presumably their temporal pattern of activity is adaptive and important to their success at northern latitudes. Cunners survive six months or more of torpor that can begin at a time not predictable by exogenous cues in the marine environment. At our study site, the date at which winter torpor commences (i.e. when seawater temperature remains below $\sim 5^{\circ}\text{C}$) can vary year to year by at least four weeks. Perhaps an endogenous mechanism sensitive to changes in day length, or to some other environmental cue, regulates the physiological processes associated with successful winter torpor. Although such a mechanism may exist in cunners, the identification of endogenous rhythms in fishes is difficult (Boujard and Leatherland, 1992).

Our findings concerning seasonal changes in the activity patterns of cunners have implications for estimating the size of their populations. For example, population estimates based on visual surveys by divers should take into account that, depending on when the survey is conducted, a significant and variable proportion of the population will be out of sight, under cover. Significant errors in estimates of population size are likely, and errors will not be consistent for different times of the year. This caution may apply to other species with similar behavior patterns.

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