Japan. J. Ichthyol.
42(3/4): 261–267, 1995

魚類学雑誌
42(3/4): 261–267, 1995

Twilight Migrations of the Temperate Japanese Surfperch *Neoditrema ransonneti* (Embiotocidae)

Makoto Sakurai and Akinobu Nakazono

Fisheries Laboratory, Faculty of Agriculture, Kyushu University,
6–10–1 Hakozaki, Higashi-ku, Fukuoka 812, Japan

(*Received March 10, 1995; in revised form July 11, 1995; accepted September 12, 1995*)

Abstract Daily twilight migrations of the Japanese surfperch, *Neoditrema ransonneti*, a temperate rocky reef inhabitant, are described on the basis of studies around Fukudomari Harbor, Saiki Bay, Kyushu. Migrations occurred from late August through January, being the time of year of high *N. ransonneti* abundance in nearshore waters. At dusk, fish moved from coastal rocky reefs, where they had been diurnally active, to the harbor, either solitarily or in schools. Movement into the harbor began on average, 30.4 min. before sunset, the last arrival taking place 10.2 min. after sunset. During nighttime, the fish remained in the harbor, subsequently. The beginning their migration to open waters some 27.6 min. before sunrise. Migration routes were established up to at least 100 to 150 m from the harbor. The sequence of migratory behavior at the entrance of the harbor was categorized according to certain behavioral events, such as migration in schools and migration in procession (a long dense school). Each behavioral event began and ceased with precise timing relative to sunset or sunrise, the effect of variations in underwater illumination on each event being small. Practically all of the individuals (approximately 48,000) observed around the harbor were considered to migrate.

It is well known that many tropical and temperate reef fishes perform extensive twilight migrations between foraging areas and refuges (Hobson, 1972, 1973; Ebeling and Bray, 1976; Hobson et al., 1981; Helfman, 1986). Some migrate between nocturnal feeding grounds and diurnal resting locations, e.g., certain atherinids (Hobson and Chess, 1973; Major, 1977), pempherids (Fishelson et al., 1971; Gladfelter, 1979), priacanthids (Hobson, 1972), pomadasyids (Hobson and Chess, 1976; Ogden and Ehrlich, 1977; McFarland et al., 1979; Helfman et al., 1982) and clupeids (Hobson, 1973); others migrate between diurnal feeding grounds and nocturnal resting places, e.g., certain pomacentrids (Hobson et al., 1981), scarids (Ogden and Buckman, 1973; Dubin and Baker, 1982), and acanthurids (Mazeroll and Montgomery, 1995). Although twilight migrations by tropical species have been described as predictable movements along established routes at precise times (Hobson, 1973; Helfman, 1986), it has been suggested that comparable precision is lacking in temperate water species (Ebeling and Bray, 1976; Helfman, 1986).

To examine the degree of precision in the twilight migration of a temperate species, diel movements of the Japanese surfperch, *Neoditrema ransonneti*, were studied in Saiki Bay, northern Kyushu (33°03′N, 131°59′E). *Neoditrema ransonneti* is a diurnal planktivore attaining about 13 cm in fork length, that has a recorded range from southern Hokkaido to mid Kyushu, as well as along the southern shores of Korea (Tarp, 1952; Hayase and Tanaka, 1980a, b). After initial observations of this species moving from a diurnal feeding area offshore to a nocturnal refuge inside the harbor, a formal study was undertaken to clarify the details of such movements.

Materials and Methods

Study area

The study was performed mainly in and around Fukudomari Harbor, located on the northern coast of Saiki Bay, Oita Prefecture, Kyushu, Japan (Fig. 1). Fukudomari Harbor is protected by two concrete breakwaters, separated by a narrow entrance, 18 m wide (Fig. 2A). The southern breakwater is 120 m long, and the western breakwater 50 m long. The maximum depth in the harbor was six meters.

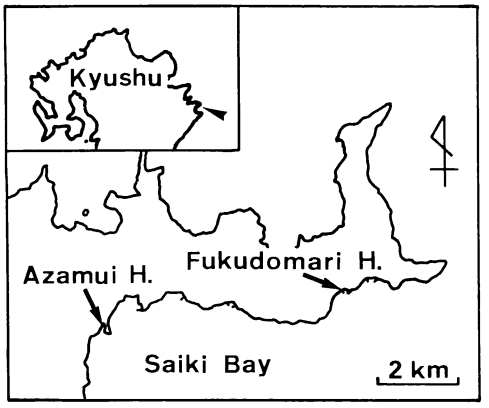

Fig. 1. Maps of the study areas on the northern coast of Saiki Bay, Kyushu, Japan, showing the locations of Fukudomari and Azamui Harbors.

The bottom around the harbor being rocky, except for a sandy area on the western side. Observations were made primarily on the entrance of Fukudomari Harbor and on the rocky reef surrounding the harbor. Additional observations were made at Azamui Harbor, 7.8 km west of Fukudomari Harbor (Fig. 1). The study was performed from September 1986 through August 1987, during which time the water temperature varied between 10.2°C and 27.2°C.

Methods of observations

To examine the general habitat and twilight migration patterns, individual numbers and locations of the fish were recorded during the day and night, as well as in the twilight periods. Observations were made almost every day from October through December 1986, but at irregular intervals in September 1986 (number of observations=80), and from January through August 1987 (number of observations=40). Within the periods when twilight migration occurred, general migratory behavior was observed at dusk on 32 days and at dawn on 10 days. Of these, 18 dusk and 7 dawn migrations were recorded in detail, including individual numbers, time and underwater illumination. The latter observation days

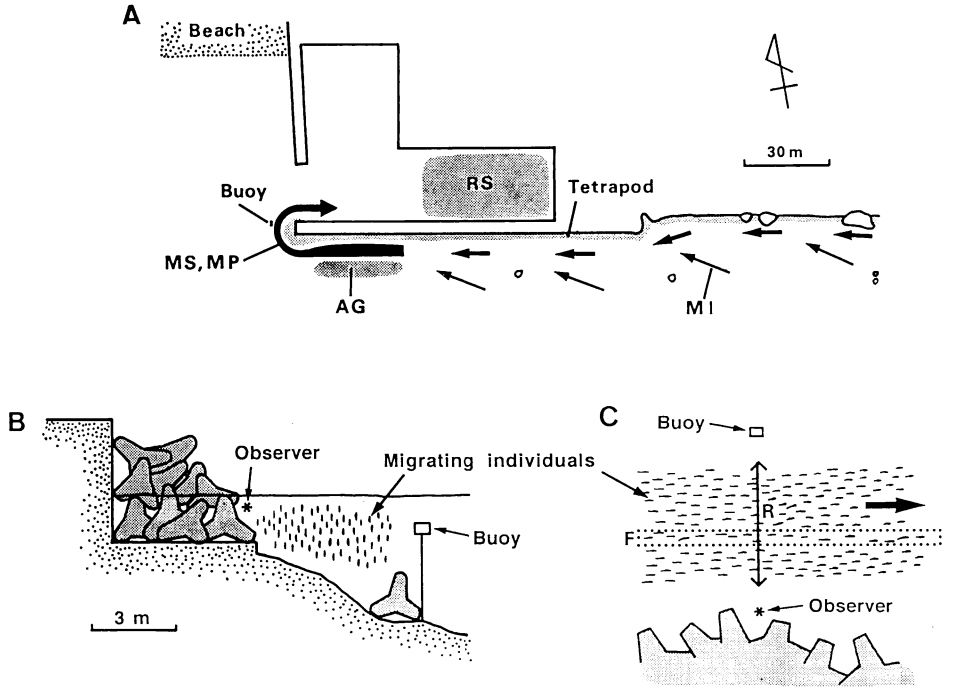

Fig. 2. General outline of the dusk migration pattern at Fukudomari Harbor and methods of counting the migrating individuals. A) Routes and behavioral sequence during dusk migration: *MI*—routes of migrating individuals; *AG*—aggregation on seaward aspect of southern breakwater; *MS*, *MP*—moving into harbor in schools or in procession; *RS*—resting site at night. B) Horizontal view of observation line (*OL*, between tetrapods and buoy), across which most migrating individuals passed. C) Vertical view of OL and methods of counting individuals (see text). (Arrow indicates direction of fish movement.)

included fine, cloudy and rainy weather.

Most of the migrating fish passed between a buoy anchored at mid-depth, five meters offshore near the tip of the southern breakwater and seawardly-positioned tetrapods (observation line=OL, Fig. 2B). The number of fish passing the OL in each five minute period was recorded for 1–5 hours (including the twilight periods). When the number of individuals exceeded one hundred per minute, it was estimated from the approximate number of fish on the OL at a single point in time (vertical plane; a rank of the school=R, Fig. 2C) multiplied by the number of fish crossing the OL per minute (horizontal plane; a file of the school=F, Fig. 2C). At the same time, underwater illumination (lux) was measured every five minutes using an illuminationmeter positioned 0.5 m from the surface at the center of the OL.

Nighttime observations (18:00–21:30) in Fukudomari Harbor were carried out on 29 October, and 5 and 11 December 1986, to examine fish sheltering sites and general behavior in the refuge. Migration routes were established by following the paths of individuals traveling from the harbor at dawn, until lost sight of.

The number of individuals and initial and terminal times of the dusk migrations were also recorded at the entry of Azamui Harbor on two days in November and December 1986, using methods similar to those described above.

In order to avoid SCUBA diver-effect on fish behavior, observations were made by snorkeling, except for nighttime observations within the harbor. Data were recorded on waterproof paper and an underwater camera provided film documentation.

Results

Twilight migrations occurred from late August through January, being the time of year of high *Neoditrema ransonneti* abundance along the shore near Fukudomari Harbor. The species was active by day, either individually or in schools, above rocky reefs offshore from the harbor, averaging 645 (range, 117–1925, SD=606.2, $n=7$) along a 250×5 m transect. During evening twilight the fish migrated into the harbor, where they remained until returning to their offshore feeding area during morning twilight. Migrations were not seen from February through early August, when few *N. ransonneti* occurred in the area.

Fig. 3. *Neoditrema ransonneti* in procession during dusk migration.

Dusk migration

Migration routes and behavioral sequences at dusk migration are summarized in Figure 2A. About 60 to 50 min. before sunset, solitary individuals and schools of 20–100 individuals began to swim toward the harbor from the rocky reef located to the east and south-east (Fig. 2A: MI), following virtually the same routes near the breakwater each day. No individuals were observed coming from the west or south-west. Between two and 15 m offshore from the southern breakwater, all migrating individuals stopped and eventually formed aggregations (Fig. 2A: AG). About 30 min. before sunset, these fish began to swim toward the harbor.

Migrating behavior observed at the OL included three recognizable features. (i) Migration in schools. Initially, aggregations of fish moved into the harbor, by turning right at the tip of the southern breakwater, in schools of between several to 300 fish (Fig. 2A: MS). (ii) Migration in procession. As the number of migrating fish increased, the schools combined, forming a single, very long, dense school, here defined as a procession. The procession, some 30 to 40 m long and two to five meters wide, was formed along the southern breakwater (Fig. 2A: MP, Fig. 3), and continued for an average of 22.6 min. (range, 15–35 min., $n=18$), later arrivals joining at the posterior end. Individuals in the procession kept between 10 to 80 cm apart from each other. When the procession had finished, only a small number of *N. ransonneti* remained outside of the harbor. (iii) Migration in schools following the procession. Occasionally, 10 to 300 fish in one to five schools moved into the harbor within 11 min. of the termination of

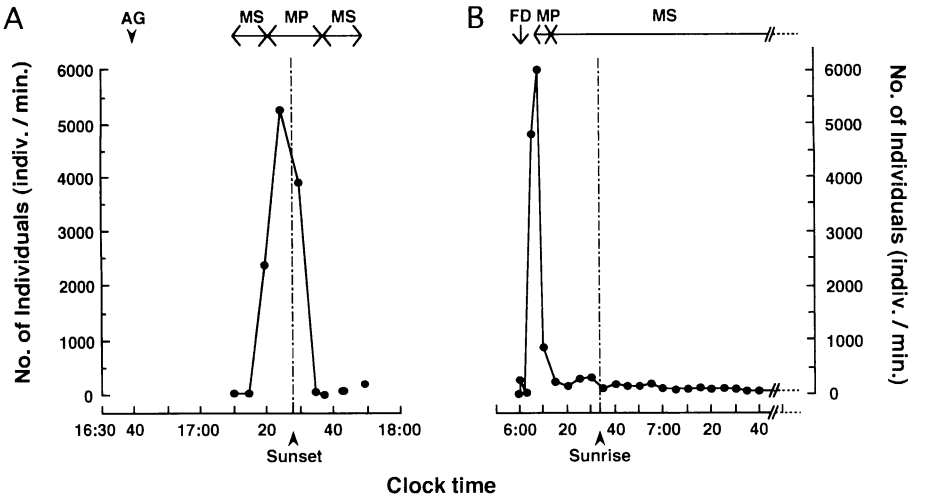

Fig. 4. Number of individuals/min. which passed the OL during dusk and dawn migrations in 1986. A) Dusk migration on 27 October. B) Dawn migration on 3 November. Dashed line indicates sunset or sunrise. Duration of each behavioral event indicated at top: *AG*—initiation of aggregation on seaward aspect of breakwater; *MS*—migration in schools; *MP*—migration in procession; *FD*—first departure from harbor.

the procession. The above three behavioral stages took, on average, 40.0 min. (range, 27–50 min., $n=11$) for over all completion. The average number of individuals counted during five dusk migrations was approximately 48,000 (range, 32,000–69,000).

The results of evening twilight observations on 27 October, 1986, are shown in Figure 4A. Aggregations appeared off the southern breakwater at about 16:40, the schools beginning to move into the harbor at 17:10. A procession was observed from 17:21 through 17:38. The maximum individual number per minute was approximately 5300, occurring at 17:25. Following the procession, 4 schools of 50 to 200 individuals entered the harbor, the last at 17:49.

To examine the consistency of the behavioral sequences during both dusk and dawn migrations, the initial and terminal migration times, and underwater illumination during each behavioral event, were recorded. During the autumn observation periods, sunset changed between 17:06 and 17:31. The average time and underwater illumination for each behavioral event are shown in Figure 5. In dusk migration (Fig. 5A), individuals, aggregating off the breakwater, began to move into the harbor 30.4 min. before sunset on average (SD=7.8, $n=8$). At this time, underwater illumination was 1220 lux (SD=550, $n=8$). The procession formed 15.9 min. before sunset (SD=9.3, $n=18$), illumination being 691 lux (SD=402, $n=18$). The procession terminated 6.6 min. after sunset (SD=6.0, $n=18$), at which time illumination was 55 lux (SD=33, $n=18$). The latest arrival time of migrating individuals was 10.2 min. after sunset (SD=6.5, $n=18$), when illumination was 35 lux (SD=23, $n=18$). Weather conditions did not influence underwater illumination at the initial and terminal times of each event, because of the low level of underwater illumination at dusk. Variations in the time, relative to sunset and underwater illumination, of each behavioral event were small.

Nighttime refuge

At night, dense aggregations of *N. ransonneti* were observed in Fukudomari Harbor (Fig. 2A: RS), where they remained motionless among the *Sargassum* vegetation or near the bottom.

Dawn migration

Early in the morning, fish migrated from the harbor to the rocky reef. Initially, a procession leaving the harbor began abruptly, continuing for an average of 9.6 min. (range, 7–18, $n=7$). Occasionally, several schools moved out just before the departure of the procession. Following the procession, schools composed of 10 to 200 individuals moved out intermittently, such migration continuing until 10:00 or 11:00. The end point of each morning migration was not clear cut.

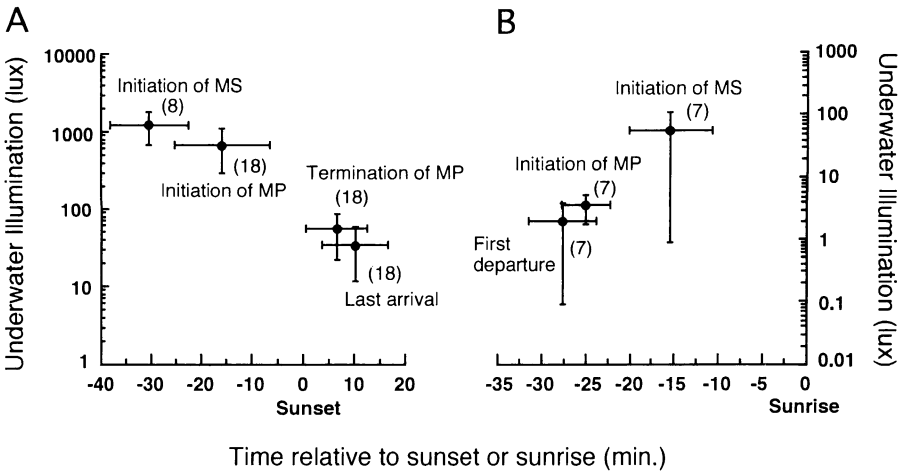

Fig. 5. Mean initiation and termination times and underwater illumination (lux) of each behavioral event at Fukudomari Harbor during dusk (A) and dawn (B) migrations. *MS*—migration in schools; *MP*—migration in procession. Times are shown relative to sunset or sunrise. Vertical and horizontal bars indicate SD. Number of observations shown in parentheses.

The results of morning twilight observations on 3 November, 1986, are shown in Figure 4B. Initial departure of individuals was observed at 06:02, when a school of 150 individuals moved out of the harbor. The procession began at 06:08 and continued till 06:15. Migration in small schools of 10 to 200 individuals followed the procession until about 11:00.

Migrating individuals swam in a south-easterly direction along the coast, reversing the dusk migration route for about 100 to 150 m. Some fish gradually decreased their swimming speed and stopped within 250 m of the harbor, where they stayed during daytime. Others moved farther out from the harbor, and were lost to sight.

During the observation periods, sunrise changed from 06:25 to 07:14. The first departure of dawn migration (Fig. 5B) occurred 27.6 min. before sunrise (SD=3.9, $n=7$), at which time illumination was 2.0 lux (SD=1.9, $n=7$). Migration in procession began 25.0 min. before sunrise (SD=2.8, $n=7$), illumination being 3.5 lux (SD=1.8, $n=7$). Migration in schools, following the procession, began 15.4 min. before sunrise (SD=1.8, $n=7$), when illumination was 55 lux (SD=20, $n=7$). Variations remained small, regardless of weather conditions.

Seasonal presence of *N. ransonneti* and migration at Azamui Harbor

The patterns of seasonal occurrence of *N. ransonneti* at Azamui and Fukudomari harbors were similar. During the period from late summer to early winter, several individuals appeared nearshore at Azamui, moving into the harbor at dusk. For example, at least several thousand fish migrated into the harbor between 16:40–17:20 (November 24) and 17:00–17:25 (December 4) in 1986. From winter to summer, however, few individuals occurred nearshore and twilight migration was not observed.

Discussion

In the temperate marine waters of California, several species migrate between foraging sites and refuges on a daily basis, including both diurnal species, such as *Chromis punctipinnis* (Hobson et al., 1981), and nocturnal species, e.g. *Xenistius californiensis* (Hobson and Chess, 1976) and *Hyperprosopon argenteum* (Ebeling and Bray, 1976). In southeastern Alaska, twilight movements have been observed in nocturnal Ammodytidae, *Ammodytes hexapterus* (Hobson, 1986). There has been little evidence presented to suggest that the twilight migrations of these species are as precisely timed or routed as those of tropical species (Hobson et al., 1981; Hobson and Chess, 1976). In fact, some studies have suggested that such precision is lacking at higher latitudes (Ebeling and bray, 1976; Helfman, 1986). The present study has shown, however, that the twilight migrations of temperate *Neoditrema ransonneti* in

Saiki Bay are comparable to those of fishes in tropical habitats.

On tropical reefs of the Marshall islands, twilight migrations of the nocturnal, planktivorous atherinid, *Pranesus pinguis*, have been reported (Hobson and Chess, 1973). Although *N. ransonneti* differs from *P. pinguis* in being diurnal, some similarities exist in the migratory behavior of the two species. Both migrate between offshore feeding areas and nearshore resting sites during twilight periods, utilizing similar routes each time. In addition, before the final movement to the resting sites, both aggregate in the shoreward part of their feeding ground.

Neoditrema ransonneti performed each component of its twilight migration within a narrow range of time and light intensity, indicating that some environmental factors trigger the initiation and ceasing of their diurnal activity. It has been suggested that increasing and decreasing underwater light levels during the twilight periods, respectively initiate and terminate the activities of coral reef fishes (Major, 1977; Gladfelter, 1979; McFarland et al., 1979; Dubin and Baker, 1982). Furthermore, an endogenous circadian rhythm is suspected (McFarland et al., 1979). A reasonable supposition, therefore, is that underwater illumination or time relative to sunset and sunrise (endogenous circadian rhythm) may determine the migration times of *N. ransonneti*, as has been proposed for tropical reef fishes.

Dusk migration was considered to be completed when the last fish passed the observation point, such taking place, on average, 10.2 min. after sunset (range, 3 min. before sunset–21 min. after sunset). Dawn migration was considered to have begun when the first fish passed the observation point, on average 27.6 min. before sunrise (range, 31–20 min. before sunrise). Diurnal damselfish, *Chromis punctipinnis*, end their dusk migration to a nocturnal resting area some 10 min. after sunset, in the warm-temperate waters of southern California (Hobson et al., 1981), almost at the same time as *N. ransonneti*.

As twilight migrations of *N. ransonneti* were also observed at Azamui Harbor, such behavior was clearly not restricted to Fukudomari Harbor, instead very likely being a widespread phenomenon. Migrations took place from August through January. During these months, several individuals inhabited the rocky reefs surrounding Fukudomari Harbor in the daytime, whereas in other months few individuals were apparent and twilight migrations were not observed. The advantages of twilight migration, with reference to effective feeding and lowered risk of predation, have been discussed by Hobson (1973, 1986), Gladfelter (1979) and Helfman (1986). It is supposed that *N. ransonneti* predators were fewer in the harbor compared with the outside reef, although zooplankton abundance in the harbor was also lower. Twilight migrations of *N. ransonneti* therefore represent adaptations to optimize resting sites, feeding areas and avoidance of predator activity.

Acknowledgments

We are very grateful to Dr. E. E. DeMartini and Dr. G. S. Hardy for their critical reading of the manuscript, and the fisherman's union of Kamiura, for providing permission and help during this research. We also thank the Fukuizumi family, who accommodated us at Azamui-cho, and two anonymous reviewers for their helpful comments on the manuscript.

Literature Cited

Dubin, R. E. and J. D. Baker. 1982. Two types of cover-seeking behavior at sunset by the princess parrotfish, *Scarus taeniopterus*, at Barbados, West Indies. Bull. Mar. Sci., 32: 572–583.

Ebeling, A. W. and R. N. Bray. 1976. Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. Fish. Bull., 74: 703–717.

Fishelson, L., D. Popper and N. Gunderman. 1971. Diurnal cyclic behaviour of *Pempheris oualensis* Cuv. & Val. (Pempheridae, Teleostei). J. Nat. Hist., 5: 503–506.

Gladfelter, W. B. 1979. Twilight migrations and foraging activities of the copper sweeper *Pempheris schomburgki* (Teleostei: Pempheridae). Mar. Biol., 50: 109–119.

Hayase, S. and S. Tanaka. 1980a. Growth and reproduction of three species of embiotocid fishes in the *Zostera marina* belt of Odawa Bay. Bull. Japan. Soc. Sci. Fish., 46: 1089–1096.

Hayase, S. and S. Tanaka. 1980b. Feeding ecology of three species of embiotocid fishes in the *Zostera marina* belt of Odawa Bay. Bull. Japan. Soc. Sci. Fish., 46: 1469–1476.

Helfman, G. S. 1986. Fish behaviour by day, night and twilight. Pages 366–387 *in* T. J. Pitcher, ed. The behaviour of teleost fishes. Croom Helm, London.

Helfman, G. S., J. L. Meyer and W. N. McFarland. 1982. The ontogeny of twilight migration patterns in grunts (Pisces: Haemulidae). Anim. Behav., 30: 317–326.

Hobson, E. S. 1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight

and darkness. Fish. Bull., 70: 715–740.
Hobson, E. S. 1973. Diel feeding migrations in tropical reef fishes. Helgoländer wiss. Meeresunters., 24: 361–370.
Hobson, E. S. 1986. Predation on the pacific sand lance, *Ammodytes hexapterus* (Pisces: Ammodytidae), during the transition between day and night in southeastern Alaska. Copeia, 1986: 223–226.
Hobson, E. S. and J. R. Chess. 1973. Feeding oriented movements of the atherinid fish *Pranesus pinguis* at Majuro Atoll, Marshall Islands. Fish. Bull., 71: 777–786.
Hobson, E. S. and J. R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., 74: 567–598.
Hobson, E. S., W. N. McFarland and J. R. Chess. 1981. Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment. Fish. Bull., 79: 1–30.
Major, P. F. 1977. Predator-prey interactions in schooling fishes during periods of twilight: a study of the silverside *Pranesus insularum* in Hawaii. Fish. Bull., 75: 415–426.
Mazeroll, A. I. and W. L. Montgomery. 1995. Structure and organization of local migrations in brown surgeonfish (*Acanthurus nigrofuscus*). Ethology, 99: 89–106.
McFarland, W. N., J. C. Ogden and J. N. Lythgoe. 1979. The influence of light on the twilight migrations of grunts. Env. Biol. Fish., 4: 9–22.
Ogden, J. C. and N. S. Buckman. 1973. Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology., 54: 589–596.
Ogden, J. C. and P. R. Ehrlich. 1977. The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). Mar. Biol., 42: 273–280.
Tarp, F. H. 1952. A revision of the family Embiotocidae (the surfperches). Calif. Dept. Fish Game, Fish Bull., 88: 1–99.

オキタナゴの薄明薄暮期の移動

櫻井　真・中園明信

大分県佐伯湾に面する温帯域に生息するオキタナゴの薄明薄暮期の日周移動を観察，記録した．日周移動が観察されたのは，多数の個体が浅瀬の岩礁に出現する秋から初冬に限られた．本種は日中は漁港周辺の岩礁で活動したが，夕方になると港方向へと移動し，日没の平均30.4分前から日没後10.2分の間に港内へ入った．これらの個体は夜間は港内で休息し，翌朝，日の出前27.6分から港外へ再び移動した．移動経路は港周辺の100–150 mの範囲では毎日同じであった．港入口での行動は，移動個体の作る群れの大きさと形状により，小群による移動，行列を成す大群による移動，行列後の小群による移動に区分できた．これらの行動の開始と終了の時刻は，日没・日の出時刻に対する時刻がほぼ一定で，この時の水中照度もそれぞれ一定していた．漁港周辺に生息するほとんどすべての個体が漁港と岩礁域の間を移動すると考えられ，港入口における計数結果より移動個体数は約48,000尾と推定された．

（〒812 福岡市東区箱崎6-10-1　九州大学農学部水産学第二講座）