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Identifying spawning behavior in Pacific halibut, *Hippoglossus stenolepis*, using electronic tags

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Synopsis

Identifying spawning behavior in Pacific halibut, *Hippoglossus stenolepis*, is particularly challenging because they occupy a deep, remote environment during the spawning season. To identify spawning events, a method is needed in which direct observation by humans is not employed. Spawning behavior of seven other flatfish species has been directly observed in their natural environment by investigators using SCUBA. All of these flatfish species display almost identical spawning behavior that follows a routine. Therefore, it is reasonable to believe that this spawning behavior occurs in other flatfish species, including Pacific halibut. As part of a larger study, we recaptured two Pacific halibut on which Pop-up Archival Transmitting (PAT) tags had been attached during the winter spawning season. Because the tags were physically retrieved, we were able to collect minute-by-minute depth records for 135 and 155 days. We used these depth data to tentatively identify spawning events. On seven separate occasions between 20 January 2001 and 9 February 2001, one fish displayed a conspicuous routine only seen during the spawning season of Pacific halibut and the routine parallels the actions of other spawning flatfish directly observed by humans using SCUBA. Therefore, we propose this routine represents spawning behavior in Pacific halibut. The second tagged fish did not display the conspicuous routine, thus challenging the assumption that Pacific halibut are annual spawners. PAT tags may prove to be a useful tool for identifying spawning events of Pacific halibut, and that knowledge may be used for improved management in the future.

Introduction

Information on the timing and location of spawning in commercially harvested fish species is frequently needed to resolve biological questions associated with the management of the fishery, to explain observed changes in the juvenile and adult populations and to plan research programs (St-Pierre 1984). Identifying and describing spawning behavior has been challenging to fishery scientists because of the relatively inaccessible environment of fishes. This leaves a gap in knowledge for proper management of many fish species.

Pacific halibut, *Hippoglossus stenolepis*, is a flatfish that inhabits the continental shelf of the United States and Canada, ranging from California to the Bering Sea, and extending into Russia and Japan. Current knowledge suggests that the spawning period for Pacific halibut is from early November to late March on spawning grounds concentrated along the continental slope at depths from 183 to 457 m. In addition to the slope, it is believed that spawning also occurs in depressions on the continental shelf. The spawning period for female halibut is characterized by a gradual shedding of the ripe ova and females spawn over an extended period as only a portion of all the eggs are ripe at any one time. Halibut are capable of spawning annually and 'apparently a high percentage, if not all, do so' (St-Pierre 1984). These conclusions are based on the winter commercial fishery from 1913 to 1924. After 1924, the commercial fishing season was closed during the winter spawning season as a protective measure, and subsequent spawning data were collected only during infrequent research cruises. Because of the scant data regarding Pacific halibut spawning, considerable debate and speculation exists concerning their spawning behavior.

Spawning behavior of seven flatfish species has been directly observed in their natural environment by investigators using SCUBA. The behavior is described for one paralychthyid, bastard halibut, *Taphops oligolepis*, off Japan (Manabe & Shinomiya 2001), and six bothids: wide-eyed flounder, *Bothus podas*, off the Azore Islands (Carvalho et al. 2003), Caribbean eyed flounder, *Bothus ocellatus*, Peacock flounder, *Bothus lunatus*, and *Bothus ellipticus* off the Netherland Antilles Islands (Konstantinou & Shen 1995), lefteye flounder, *Engyprosopon grandisquama*, off Japan (Manabe et al. 2000), and Kobe flounder, *Crossorhombus kobensis*, off Japan (Moyer et al. 1985). All of these flatfish species follow a spawning routine consisting of three stages: courtship, spawning rise, and post-spawning. During courtship, a male courts a female by swimming below or on top of her and signals his readiness to mate. If courtship is successful, it is followed by the second stage, an abrupt and steep 'spawning rise' off of the seafloor by both the male and the female. During the spawning rise, the flatfish swim vertically from the bottom, release their gametes at the apex of the rise, and then immediately return to the bottom. In the final stage, post-spawning, the male and female return to their territories and either begin feeding or bury themselves in the sand for the night.

Because this spawning behavior occurs in seven species across two flatfish families and there is no other spawning behavior documentation for flat fishes, we feel that it is reasonable to hypothesize that the spawning behavior previously described occurs in many or all flatfish species, including members of the family Pleuronectidae. However, identifying spawning behavior in Pacific halibut is particularly challenging because it occupies a rather, inhospitable, remote environment during the spawning season. Hence, a method is needed to identify spawning events in Pacific halibut in which direct observation by humans is not employed.

Pop-up Archival Transmitting (PAT) tags have been used to gather behavioral inference of fish for several years (see review in Arnold & Dewar 2001). With miniaturized on-board computers, PAT tags measure and record depth, temperature and ambient light data (for light-based geolocation). On a user-programmable date, PAT tags release from the fish, float to the surface and send low-resolution summarized data to satellites. If the tag is physically recaptured, one may obtain the high-resolution time series data.

In this paper, we examine the high-resolution depth data collected by two PAT tags that were attached to adult Pacific halibut for the duration of the spawning season. These two tags were a fortuitous bonus to a larger investigation in which Pacific halibut were tagged and released with PAT tags to test the feasibility of using the tags as a tool to investigate migration and behavior of Pacific halibut in the Gulf of Alaska (Seitz et al. 2003). Comparing the high-resolution depth data collected by PAT tags to human observed spawning behavior in other flatfish species may allow identification of spawning events in Pacific halibut, thus contributing to improved knowledge for proper management. In this paper, we do not draw quantitative conclusions, but rather present an interesting observation in the depth record of a Pacific halibut that seems to mimic directly observed spawning behavior in several other flatfish species. We feel that our observations are more than coincidental and we are disseminating these findings so other scientists investigating flatfish with electronic tags are aware of the behavior.

Materials and methods

Between 20 November 2000 and 5 July 2001, we tagged and released 14 Pacific halibut (107–165 cm FL) with Wildlife Computers (Redmond, WA) PAT tags in and around Resurrection Bay, Alaska, USA (latitude 59.89°N, longitude 149.49°W; for details, see Seitz et al. 2003). We determined sexual maturity of the fish by comparing the length of the tagged fish to sexual maturity ogives for Pacific halibut in the northern Gulf of Alaska (Clark et al. 1999). Here we report the minute-by-minute depth records for two tags that were physically recovered. We examined the depth records and tentatively identified the three stages of spawning in flatfish: courtship, spawning rises, and post-spawning activity. The proposed courtship was defined as the time during which the Pacific halibut showed a descending trend in depth after a prolonged stay at a constant depth. Courtship ended at the beginning of the proposed spawning rises, which were defined as the abrupt 'spike' in the depth record. The proposed post-spawning activity began immediately after the end of the spawning rise and was defined as the time when the Pacific halibut gradually ascended until it reached a constant or mildly fluctuating depth. The total duration of a proposed spawning event was defined as the time elapsed between the commencement of courtship and the end of the post-spawning activity. The time between spawning events was defined as the time between the end of post-spawning activity and the initiation of the next courtship behavior.

Results

We physically recaptured a total of four PAT tags, of which two were attached to Pacific halibut for the entire winter spawning season. These two tags, 00–0737 and 00–0738, were released on 20 November 2000 and provided minute-by-minute depth records for 135 and 155 days, respectively. Both fish were 130 cm FL at release; at that size in the northern Gulf of Alaska, approximately 99% of Pacific halibut are mature (Clark et al. 1999). They were recovered 20.3 and 2.5 km, respectively, from the release site. Although they were recaptured in close proximity to the release site, they did not remain in this vicinity during the winter. These fish experienced maximum depths of 502 and 466 m, respectively, within 2 weeks after their release. Depths of this magnitude do not exist in Resurrection Bay, indicating that these two fish must have migrated out of the Bay to the continental slope. Based on depth records, it appears as though after spending the winter in deep water on the slope, both fish migrated back to their summer feeding grounds in Resurrection Bay where they were recaptured. We were unable to ascertain the exact daily location of each halibut using light-based geolocation because of the low ambient light levels experienced by the fish.

During early winter of 2001, fish 00-0737 inhabited depths consistent with the continental slope (January: $\bar{X} \pm SD = 320.6 \pm 18.0$ m, range 270.0–450.0 m; February: 287.2 ± 61.0 m, range 198.0–502.0 m). While on the slope, on seven separate occasions between 20 January 2001 and 9 February 2001, fish 00-0737 displayed a conspicuous routine where it gradually moved to greater depth, abruptly ascended and abruptly descended, and then gradually ascended (Figure 1). From the temperature (not shown) and depth records during this behavior, the fish appeared to have left the bottom and swam vertically through the water column. The entire routine did not appear to start or finish at the same time everyday, but it does appear to be regularly spaced, occurring approximately every 65 h (Table 1). The depths at which the routine started and finished, differed by as little as 4 m on three occasions, but never more than 36 m (Table 1). The height of the vertical rise seemed to follow a pattern with the first and last rises being half the height of the rise in mid-cycle.

Fish 00-0738 also inhabited the contiental slope (January: 276.7 ± 34.4 m, range 126.0–318.0 m; February: 249.1 ± 29.0 m, range 142.0–294.0 m). However, the conspicuous routine observed in the depth record of fish 00-0737 was not observed in the depth record of fish 00-0738. The other two tags that were physically recaptured were not attached to halibut during the winter spawning season and neither of these tags had evidence of the conspicuous routine.

Discussion

PAT tags provide high-resolution depth data if physically recovered, which occurs with regularity

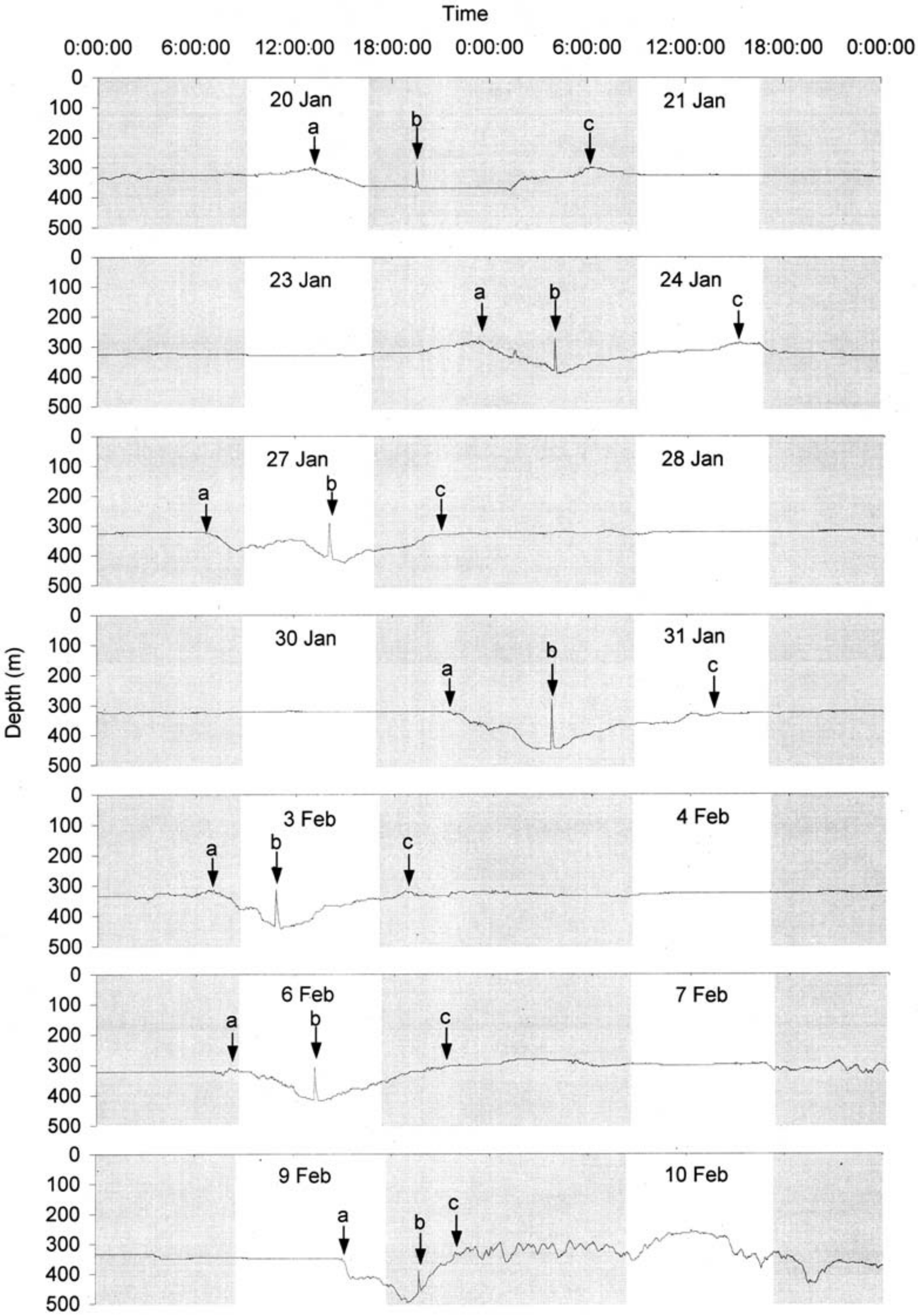

Figure 1. Proposed spawning activity for Pacific halibut 00-0737. Depth was sampled each minute; 'a' is the beginning of proposed courtship activity and the spawning routine; 'b' is the proposed spawning rise; 'c' is the end of the post-spawning activity and the spawning routine. Shaded areas are between sunset and sunrise, calculated for the estimated vicinity of the fish on the continental shelf edge (latitude 59°N, longitude 148°W).

for Pacific halibut (recovery rate = 29%, Seitz et al. 2003; Seitz unpublished data). These depth data have been used to tentatively identify spawning behavior in other species of fish. In one instance, an Atlantic bluefin tuna, *Thunnus thynnus*, on its breeding grounds performed a distinct diel oscillatory diving behavior that was seen only during the spawning season (Block et al. 2001). The authors proposed it was spawning behavior.

Similarly, the depth record of fish 00-0737 reveals a routine only seen during the spawning season of Pacific halibut and this routine parallels the actions of spawning flatfish directly observed by humans using SCUBA. Therefore, we propose this routine represents spawning behavior in Pacific halibut. We further propose that the gradual descent, the abrupt ascent and descent, and the subsequent gradual ascent seen in the depth record of PAT tagged Pacific halibut represent courtship, spawning rise, and post-spawning behavior, respectively.

The slow descent seen in the depth record of the Pacific halibut may represent the courtship described for flatfish species (Moyer et al. 1985; Konstantinou & Shen 1995; Manabe et al. 2000; Manabe & Shinomiya 2001; Carvalho et al. 2003). During courtship in these species, the male and female slowly swim together across the bottom substrate. In Pacific halibut, it appears that the fish swim toward deeper water during this courtship period.

The assumed spawning rise in Pacific halibut is of much greater magnitude than the other flatfish species. The height of the spawning rise in other species varies from as little as 15 cm (Konstantinou & Shen 1995) to 150 cm (Carvalho et al. 2003; Moyer et al. 1985). These flatfish species, with sizes no longer than 25 cm, are much smaller than the 130 cm Pacific halibut we observed. Additionally, the water depths in the other studies only ranged from 6 to 23 m prohibiting spawning rises equal to those of Pacific halibut. Spawning rises may serve to confuse predators of the mating adults as well as a means of dispersal for pelagic eggs (Konstantinou & Shen 1995). In the case of Pacific halibut, the latter seems more plausible as mature halibut have few natural predators. We propose that the depth of the apex of the spawning rise is a means for the female to vertically position the eggs and the subsequent drifting larvae in the water column. Correct depth selection for egg release may ensure onshore transport into coastal juvenile nursery grounds by the prevailing current (Bailey & Picquelle 2002).

Table 1. Timing and depths of proposed spawning activity by Pacific halibut 00-0737. The duration of the proposed spawning event includes the courtship, the spawning rise, and the post-spawning periods. Time between spawnings is the time elapsed between the end of one post-spawning period and the beginning of the next courtship period.

Date	Start Time	Finish Time	Start depth (m)	Finish depth (m)	Total duration (hh:mm)	Courtship duration (hh:mm)	Post-spawning duration (hh:mm)	Time between spawnings (hh:mm)
Proposed spawning event								
20 Jan	13:22	06:10	302	298	16:48	06:07	10:31	
24 Jan	23:42	15:17	294	286	15:35	04:16	11:08	65:32
27 Jan	06:33	22:01	322	326	15:28	07:29	07:43	63:16
31 Jan	21:24	13:37	322	330	16:13	06:17	09:44	71:23
03 Feb	07:02	18:38	314	318	11:36	03:41	07:35	65:25
06 Feb	08:03	21:20	310	302	13:17	05:05	07:57	61:25
09 Feb	14:59	22:36	350	314	07:37	04:40	02:49	65:39
mean			316	311	13:47	05:22	08:12	65:26
SD			18	16	03:16	01:19	02:46	03:21
Spawning rise								
20 Jan	19:29	19:31	19:39	366	294	370	00:10	72
24 Jan	03:58	04:02	04:09	382	270	390	00:11	112
27 Jan	14:02	14:07	14:18	398	286	410	00:16	112
31 Jan	03:41	03:45	03:53	450	282	442	00:12	168
03 Feb	10:43	10:48	11:03	430	310	442	00:20	120
06 Feb	13:08	13:10	13:23	414	302	418	00:15	112
09 Feb	19:39	19:40	19:47	462	390	458	00:08	72
Mean				415	305	419	00:13	110
SD				35	40	31	00:04	33

After the spawning rise, the proposed spawning routine ends with a slow ascent back to approximately the pre-spawning depth, which may serve two main purposes. First, the flatfish whose spawning behavior has been observed displayed territoriality (Moyer et al. 1985; Konstantinou & Shen 1995; Manabe et al. 2000; Manabe & Shinomiya 2001; Carvalho et al. 2003). This slow ascent may be a return to each individual's territory after being displaced by the courtship and spawning activity. This seems plausible because halibut are known to display territoriality while on summer feeding grounds (Hooge & Taggart 1993). A second explanation, though not mutually exclusive, is that the slow ascent provides a chance for the male to 'check' the female's abdominal area (Konstantinou & Shen 1995). In B. *ocellatus*, if the female's abdominal area was swollen after spawning, the male would usually attempt another spawning rise. If the abdomen was flat, the male would move on to another female.

Although the proposed spawning behavior of the Pacific halibut in this study is similar in many respects to the spawning behavior of other flatfish, it differs markedly in one aspect. All but one of the flatfish in the previous studies commenced courtship behavior approximately 1 h before sunset (Konstantinou & Shen 1995; Manabe et al. 2000; Manabe & Shinomiya 2001; Carvalho et al. 2003). Following courtship, spawning usually occurred around sunset, after which the fish would bury themselves in the sand for the night. In contrast to this pattern, during a 3 day observation period, *C. kobensis* spawned in the middle of the afternoon (Moyer et al. 1985), just prior to high tide. The spawning events by the single Pacific halibut in this study do not appear to be correlated to sunrise/sunset events (Figure 1). Because the smaller flatfish inhabit shallow water, they may spawn at sunset when there is less ambient light to reduce the risk of visual predation to the eggs or themselves (Konstantinou & Shen 1995). The halibut in this study was in water approximately 300–400 m deep where there is minimal ambient light, thus it was unnecessary for the fish to be concerned with visual predation. Unfortunately, we are unable to examine the possibility of a correlation of Pacific halibut spawning events with tidal events. This is because accurate tidal times in the northern Gulf of Alaska rely upon accurate location estimates (D. Musgrave, University of Alaska Fairbanks, personal communication) and we are unable to determine the fish's exact location. Although we found no evidence of correlation with solar or tidal events, the regular spacing between proposed spawning events closely corresponds to the ovulatory interval, or the time needed to hydrate a batch of eggs, in the Pacific halibuts' congener, Atlantic halibut, *Hippoglossus hippoglossus* (36–76 h; Finn et al. 2002). Therefore, the timing of spawning events in Pacific halibut may not be dictated by external cues as in other flatfish species, but rather internal physiological processes.

Although both fish in this study were of equal size and almost certainly sexually mature (Clark et al. 1999), only one displayed the proposed spawning behavior, which questions the current assumption that adult Pacific halibut spawn annually (St- Pierre 1984). Currently, the halibut stock is managed as annual spawners, even though this assumption has been challenged (Novikov 1964; Bell 1981). Our study further challenges the current management assumption that the spawning season 'could last a considerable period of time' for individual halibut (St-Pierre 1984). The proposed spawning events for fish 00-737 only occurred seven times during a period of 20 days. Twenty days is a relatively brief period of time and we are unable to ascertain whether these spawning rises resulted in successful spawning events. 'Unsuccessful' spawning rises that did not result in the release of gametes were observed 71 and 53% of the time in *B. podas* (Carvalho et al. 2003) and *B. ocellatus* (Konstantinou & Shen 1995). Success rates in this range would reduce the number of successful spawning events to three or four times per spawning season for Pacific halibut.

Ours is not a quantitative study supported by statistically based conclusions and direct observation of Pacific halibut spawning behavior. We want to generate discussion about an interesting observation from the depth record of Pacific halibut that seems to parallel directly observed behavior in several closely related species. We feel that our observations are more than coincidental. We want these findings made public now, rather than waiting for a quantitative study, so other scientists investigating flatfish with electronic tags are aware of the behavior and will look in their depth records for similar behavior. For instance, numerous electronically tagged Greenland turbot, *Reinhardtius hippoglossoides*, have displayed a similar depth spike on several occasions in their depth records similar to those of the Pacific halibut in this paper (Jim Ianelli, Alaska Fisheries Science Center, NOAA Fisheries, Seattle, Washington, USA, personal communication).

Using PAT tags to identify spawning activity in Pacific halibut appears to be a promising technique. For future spawning studies, we must ground truth the proposed spawning behavior by direct observation with a Remotely Operated Vehicle (ROV) or a submersible. If we are able to ascertain that the behavior is indeed spawning, we also may use a less expensive electronic archival tag to sample depth. Archival tags collect the same data as PAT tags, but must be physically recovered to retrieve the data. With current physical recovery rates of PAT tags archival tags at 29%, may be advantageous for identifying spawning activity because some models cost less than 10% of a PAT tag. By positively identifying spawning events in electronic tag data sets, we can improve our knowledge of Pacific halibut spawning behavior for improved management in the future.

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References

Arnold, G.P. & H. Dewar. 2001. Electronic tags in marine fisheries research: a 30-year perspective. pp. 7–64. *In*: J. Sibert & J.L. Nielsen, (eds), Electronic Tagging and Tracking in Marine Fisheries, Kluwer Academic Publishers, Dordrecht, The Netherlands.

Bailey, K.M. & S.J. Picquelle. 2002. Larval distribution of offshore spawning flatfish in the Gulf of Alaska: potential transport pathways and enhanced onshore transport during ENSO events. Mar. Ecol. Prog. Ser. 236: 205–217.

Bell, F.H. 1981. The Pacific halibut, the resource, and the fishery. Alaska Northwest Publishing Company, . 267 pp.

Block, B.A., H. Dewar, S.B. Blackwell, T.D. Williams, E.D. Prince, C.J. Farwell, A. Boustany, S.L.H. Teo, A. Seitz, A. Walli & D. Fudge. 2001. Migratory movements, depth preferences and thermal biology of Atlantic bluefin tuna. Science 293: 1310–1314.

Carvalho, N., P. Afonso & Santos. 2003. The haremic mating system and mate choice in the wide-eyed flounder, *Bothus poda*. . Environ. Biol. Fish. 66: 249–258.

Clark, W.G., S.R. Hare, A.M. Parma, P.J. Sullivan & R.J. Trumble. 1999. Decadal changes in growth and recruitment of Pacific halibut (*Hipposlossus stenolepis*). Can. J. Fish. Aquat. Sci. 56: 242–252.

Hooge, P.N. & S.J. Taggart. 1993. Home range and movement patterns of Pacific halibut *(Hipposlossus stenolepis)*: There's no place like home. Am. Zool. 33: 128A.

Finn, R.N., G.C Østby, B. Norberg & H.J. Fyhn. 2002. *In vivo* oocyte hydration in Atlantic halibut (*Hippoglossus hippoglossus*), proteolytic liberation of free amino acids, and ion transport, are driving forces for osmotic water influx. J. Exp. Biol. 205: 211–224.

International Pacific Halibut Commission (IPHC). 1998. The Pacific Halibut: biology, fishery and management. IPHC Technical Report 40. 63 pp.

Konstantinou, H. & D.C. Shen. 1995. The social and reproductive behavior of the eyed flounder, *Bothus ocellatus*, with notes on the spawning of *Bothus lunatus* and *Bothus ellipticus*. Environ. Biol. Fish. 44: 311–324.

Manabe, H., I. Miyuki & A. Shinomiya. 2000. Mating system of the lefteye flounder, *Engyprosopon grandisquama*. Ichthyol. Res. 47: 69–74.

Manabe, H. & A. Shinomiya. 2001. Two spawning seasons and mating system of the bastard halibut, *Tarphops oligolepis*. Ichthyol. Res. 48: 421–424.

Moyer, J.T., Y. Yogo, M.J. Zaiser & Tsukahara. 1985. Spawning behavior and social organization of the flounder *Crossorhombus kobensis* (Bothidae) at Miyake-jima, Japan. Jap. J. Ichthyol. 32: 363–367.

Novikov N.P., 1964. Basic elements of biology of the Pacific halibut (*Hippoglossus stenolepis* Schmidt) in the Bering Sea. pp. 175–219. *In*: P.A. Moiseev (ed.), Soviet Fisheries Investigations in the Northeastern Pacific, Part V. U.S. Department of Commerce/NTIS, Washington DC, USA.

Seitz, A.C., D. Wilson, B.L. Norcross & J.L. Nielsen. 2003. Pop-up archival transmitting (PAT) tags: a method to investigate the migration and behavior of Pacific halibut *Hippoglossus stenolepis* in the Gulf of Alaska. Alaska Fish. Res. Bull. 10: 124–136.

St-Pierre G., 1984. Spawning location and season for Pacific halibut. IPHC Sci. Rep. 70: 46.