Abstract—Field experiments were conducted to test the hypotheses that Pacific halibut (*Hippoglossus stenolepis*) display small-scale spatial structure within longline catches, relative to other species and empty hooks, or within-species based on sex or length. Sequential hook-by-hook inventories, along with length and sex data, were taken at thirty-one survey stations. Two-dimensional spatial statistics were used to test for 1) aggregation, defined as the clustering of individuals within a given demographic of size or sex over small intervals of distance; and 2) segregation, defined as the sequential occurrence of individuals within a given demographic of size or sex, uninterrupted by other observations, irrespective of the distance between individuals. Statistically significant structure was detected within catches that is more commonly associated with fish length than sex. Significant spatial structuring occurred at 60% of all stations tested. Significant aggregation of halibut of legal length for commercial retention (≥82 cm) was detected at 44% of stations and aggregation of sublegal-size halibut was detected at 11%. Male- and female-based aggregations were observed at 22% and 11% of stations, respectively. Significant segregation of females was observed at 20% of stations, male segregation occurred at 8% of stations, and segregation by size at 16% of stations. Understanding small-scale spatial structure within longline catches may help us interpret changes in survey and commercial catch data. If structure is generated by behavior, then observed size-at-age or relative sex-ratios may be biased relative to underlying distributions. Although physical processes such as gape limitation should remain stable over the time, dynamic processes may be spatially and temporally variable.

Length and sex effects on the spatial structure of catches of Pacific halibut (*Hippoglossus stenolepis*) on longline gear

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Pacific halibut (*Hippoglossus stenolepis*) support a valuable fishery in the eastern Pacific Ocean that has been monitored and managed by the International Pacific Halibut Commission (IPHC) since 1923. The IPHC's numerical stock assessment model (Clark and Hare, 2006) relies upon commercial catch-per-unit-of-effort (CPUE) data, and length-at-age, sex ratio, and maturity data collected during summer (May–August) longline surveys conducted from southern Oregon through the western Aleutian Islands, and northward along the continental shelf edge from the eastern Aleutian Islands to the U.S.-Russian border. Estimation of female spawning stock biomass (SSB_f) and sex ratios in the commercial catch and within the total biomass are important aspects of the assessment. These ratios are expected to be biased at any given size or age because halibut display sexually dimorphic growth (Clark et al., 1999) and the current minimum legal commercial size is above the male size at 100% maturity and below female size at 50% maturity (T. Loher, unpubl. data). However, sex ratios in the commercial catch cannot be obtained through catch sampling because halibut are eviscerated before landing. Instead, estimation is accomplished by applying sex ratios observed in surveys to the harvest data (Clark, 2004). This should produce accurate stock metrics as long as commercial catch demographics are the same as in the survey. However,

there are numerous aspects of stock structure that may be exploited in order to maximize CPUE and could cause decoupling between commercial and survey sex ratios.

In general, any process influenced by fish size or that results in the spatial partitioning of individuals within cohorts can influence catch demographics. Løkkeborg and Bjordal (1992) suggest that local spatial distribution, the size of individuals, effective feeding range, the mix of species present, relative competitive abilities, and the configuration of sampling gear, all contribute to longline catch-composition. Demographic partitioning is common in species that redistribute for reproduction (Moyer et al., 1985; Hannah et al., 2002), and seasonal migration between summer feeding grounds and winter spawning grounds is well documented for Pacific halibut (St. Pierre, 1984; Loher and Blood, 2009; Seitz et al., 2011). Size-specific dispersal capabilities (Dorazio et al., 1994) and sex-specific use of spawning grounds (Robichaud and Rose, 2003) have been demonstrated for other teleosts, and analyses indicate that commercial fishing periods for Pacific halibut may allow for interception fisheries that take advantage of seasonal migration (Loher, 2011). Given that commercial fishermen have long asserted the existence of size-structured aggregations of Pacific halibut, and that density-dependent social facilitation and size-

dependent feeding hierarchies have been demonstrated empirically (Stoner and Ottmar, 2004), the possibility for intracohort spatial structure deserves additional attention.

The aim of the present study was to examine whether significant levels of spatial structure were detectable within a small subsample of IPHC longline survey catches. Specifically, we sought to examine whether halibut catch is spatially structured relative to body size, sex, or the other species present. Although the longline survey has been conducted with standardized gear since 1984, data have not been collected with the spatial resolution required to test these hypotheses. Historical survey data are at the "skate level" (i.e., all fish collected on a single skate of gear (100 hooks) are pooled on deck and subsequently processed in haphazard order). In the present study, sequential hook-by-hook censuses were taken and subjected to one-dimensional spatial analysis.

Materials and methods

Sampling

Field sampling was conducted during the IPHC's standardized setline survey in June 2006. Longline gear consisted of six skates of groundline tied end-to-end, with each skate measuring 549 m and having one-hundred 16/0 circle-hooks secured by 0.6–1.2 m gangions spaced 5.5 m apart. Each hook was baited with semibright chum salmon (*Oncorhynchus keta*). Longline sets were conducted at pre-established stations located along the eastern Aleutian Islands, Alaska (Fig. 1). Gear was never set before 0500 hours and was allowed to soak for a minimum of five hours before being hauled back. Upon haul-back, a sequential hook-by-hook inventory (i.e., 600 hooks per set) was attempted, during which each hook was designated as either empty or containing a halibut or other species. For every halibut captured, length was determined and its position on the longline was recorded. Sex was determined by dissection for all commercially caught legal-size (≥82 cm fork length [FL]) individuals. For sublegal-size fish, sex was determined for only 36% of the individuals on each set because we were not granted approval to sacrifice sublegal-size halibut outside of the standard survey protocol. Hereafter, "known" sex will refer to the proportion of the sampled population for which sex identification by dissection was performed.

A total of 31 stations were sampled between 1 June and 24 June 2006. Five stations at which fewer than 25 halibut were captured were eliminated from analyses. A sixth station was eliminated because all but one fish
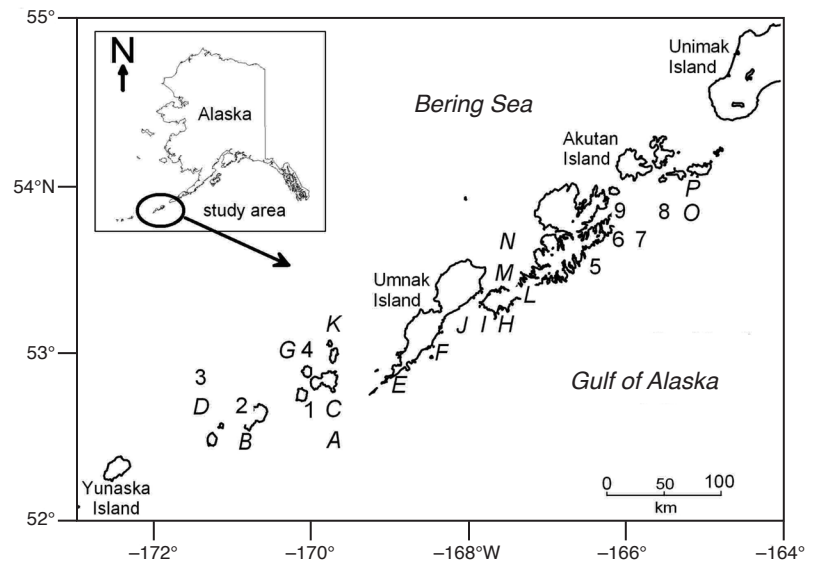
Figure 1

International Pacific Halibut Commission survey stations that were sampled to test for spatial structure in Pacific halibut (*Hippoglossus stenolepis*) longline catches. Full 600-hook inventories of all halibut, bycatch, and empty hooks were conducted at numbered stations, and the halibut data were subsequently subjected to tests of spatial aggregation with nearest neighbor analysis. At stations indicated by letters, the position of each halibut on the longline was recorded, but not of empty hooks and bycatch; for these stations, and for all numbered stations, runs rests were performed to test for sequential segregation within the halibut population.

were sublegal-size and therefore also predominantly of unknown sex. Twenty five stations (Fig. 1; Table 1) remained that were amenable to statistical analysis; runs rests (RT; described subsequently) were conducted for all of these stations. Rapid hauling rate or other logistical constraints precluded full 600-hook inventories at 16 of the aforementioned stations. Thus, for only nine stations (Fig. 1; Table 1) were both RT and nearest neighbor analysis (NNA; described subsequently) possible.

Statistical analyses

Spatial structuring of halibut on longlines was examined by using two one-dimensional statistical analyses, treating each longline as a transect and hook-status as events. Here, we make an explicit distinction between "aggregation" and "segregation." Aggregation will refer to significant physical clustering of an event type with respect to linear distance, irrespective of whether other event types were also observed with those clusters. Segregation will indicate sequential occurrence of an event type in nonrandom sequence, irrespective of the distance between observations. Segregation indicates that the demographic is "undiluted" by other population segments, but does not necessarily imply that individuals occur in close proximity. Note that the

tests for each phenomenon are independent from one another; detection of significant aggregation does not imply segregation, nor does detection of segregation indicate aggregation.

Spatial aggregation analysis   Nearest neighbor analysis (NNA), was performed as described by Selkirk and Neave (1984) to test for significant spatial aggregation of the following segments of the sampled population: 1) all halibut; 2) halibut too small to be legally retained by the commercial fishery (i.e., "sublegal-size"; <82 cm FL); 3) halibut large enough to be legally retained by the commercial fishery (i.e., "sublegal-size"; ≥82 cm FL);

4) known female halibut; and 5) known male halibut, where "known" sex refers only to those individuals that were dissected. NNA was performed for all stations at which full 600-hook inventories were performed. It was the preferred test because the distance between events is taken into consideration. In short, NNA tests not only whether the tested population segments are "interrupted" by one another, but also whether they are interrupted by empty space; therefore, it is a true spatial statistic. NNA generates a scaled nearest neighbor distance (NND) that describes the degree of aggregation relative to the scale of measurement and compares that to transect-specific lower and upper critical limits at the

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Table 1

Number of Pacific halibut (*Hippoglossus stenolepis*) captured at 25 locations in Alaska and the significance associated with tests for spatial aggregation (nearest neighbor snalysis; NNA) and sequential segregation (runs test; RT), on a station-by-station basis, for five halibut event-types: all halibut; halibut large enough to be legally retained in the commercial fishery (legal size); halibut too small to be legally retained in the commercial fishery (sublegal size); male; and female. Refer to Figure 1 for station locations. NNA was performed only where complete information regarding the presence and position of all empty hooks was available; "**A**" indicates significant ($P \leq 0.05$) spatial aggregation and "R" a random distribution. Individual P-values are listed for RT; values in bold indicate $P \leq 0.05$. RT results are reported for sublegal-size but not legal-size fish, because the only alternative to sublegal is legal. For sex-specific tests, only a proportion of individuals were known-sex because only legal-size fish were dissected. The final line indicates the percentage of stations at which either significant aggregation (NNA) or segregation (RT) was detected for each test category; some form of spatial structure was observed at 60% of all stations.

Station	No. of halibut	Spatial aggregation					Sequential segregation		
		all	legal	sublegal	male	female	sublegal	male	female
1	25	**A**	**A**	**A**	**A**	R	0.944	0.968	0.992
2	62	R	R	R	R	**A**	0.085	0.430	0.542
3	96	R	R	R	R	R	0.308	0.064	0.667
4	39	R	R	R	**A**	R	0.912	0.242	0.992
5	49	**A**	R	R	R	R	0.603	0.920	0.187
6	44	R	**A**	R	R	R	0.757	0.734	0.401
7	97	R	**A**	R	R	R	0.689	0.976	0.682
8	74	R	**A**	R	R	R	**0.001**	0.174	0.764
9	102	R	R	R	R	R	**0.041**	0.363	0.087
A	34	—	—	—	—	—	0.234	0.936	0.110
B	107	—	—	—	—	—	0.358	0.107	**0.017**
C	43	—	—	—	—	**—**	**0.001**	0.250	0.051
D	106	—	—	—	—	—	0.509	0.184	0.849
E	49	—	—	—	—	—	0.332	0.624	**0.050**
F	99	—	—	—	—	**—**	**0.032**	0.562	**0.040**
G	137	—	—	—	—	—	0.441	**0.036**	0.726
H	62	—	—	—	—	—	0.818	0.509	0.342
I	73	—	—	—	—	**—**	0.373	0.841	0.107
J	31	—	—	—	—	—	0.834	**0.028**	**0.031**
K	208	—	—	—	—	—	0.401	0.549	0.332
L	66	—	—	—	—	—	0.435	0.697	0.535
M	33	—	—	—	—	—	0.589	0.928	0.818
N	80	—	—	—	—	**—**	0.103	0.317	**0.026**
O	76	—	—	—	—	—	0.516	0.912	0.347
P	85	—	—	—	—	—	0.156	0.944	0.689
% significant		22.2	44.4	11.1	22.2	11.1	16.0	8.0	20.0

desired statistical significance level (here, *P*=0.05). NND less than the lower critical value indicates significant aggregation and NND greater than the upper critical value indicates significant overdispersion; random distribution is indicated by NND between or equal to the critical values.

Sequential segregation analysis Runs test (RT; Barton and David, 1958) was performed as described by Upton and Fingleton (1985) to test for significant segregation of 1) sublegal-size relative to legal-size halibut; 2) known males relative to females and individuals of unknown sex; and 3) known females relative to males and individuals of unknown sex. RT is a bivariate analysis in which a significant result indicates "departure from complete randomness" but does not indicate the direction of that nonrandomness; i.e., whether the events are segregated or overdispersed. Results of tests for segregation-by-length will be reported with respect to sublegal-size halibut but not for legal-size halibut, because reporting both would be redundant. Results are reported independently for male and female halibut because a third alternative (unknown sex) was possible.

Results

Spatial aggregation

On the majority of full hook-inventory sets, halibut were randomly dispersed with little clustering relative to empty hooks and bycatch: significant aggregation of halibut was found on 22% of stations (NNA; Table 1). The tendency to aggregate appeared to be size-dependent, with 44% of the sets showing significant aggregation within the legal-size segment of the halibut catch and only 11% showing aggregation of sublegal-size fish. Known male and female aggregations were significantly detected on 22% and 11% of sets, respectively. For the sets on which the fish were not aggregated, distributions were always spatially random as opposed to overdispersed (Table 1).

Sequential segregation

Sixteen percent of the sets displayed significant (RT; *P*≤0.05) halibut segregation by length, a rate somewhat lower than that observed for aggregation of legal-size halibut and higher than aggregation of sublegal-size fish (Table 1). Segregation of known males was observed on 8% of sets and female segregation on 20%. Comparison of NNA and RT results for stations upon which both tests were conducted rarely demonstrated simultaneous spatial aggregation and sequential segregation for the same population segment. Significant segregation within a given population segment was typically observed at different stations from those at which significant aggregation was detected (Table 1). Overall, some form of significant spatial structure was detected at the majority (60%) of stations.

Discussion

Our observation of significant spatial structure within the majority of longline catches examined is consistent with Clark's (2004) concern that the demographics of commercial catch may vary from survey data in undetectable ways. In particular, aggregation may allow the commercial fleet to selectively target females and the fastest-growing members of their cohorts, yielding sex ratios that differ from sex ratios encountered during surveys at any given combination of size and age. In the current analysis, aggregation based on length was more commonly detected than aggregation by sex, similar to prior wild-capture (Løkkeborg and Bjordal, 1992) and laboratory (Stoner and Ottmar, 2004) results. Patches of larger fish may occur because larger size translates into greater swimming speed, feeding range, and a likelihood of encountering bait, and because of competitive dominance. Patches of sublegal-size halibut may form owing to higher feeding motivation and more effective search patterns (Stoner and Ottmar, 2004); alternatively, some areas may simply represent size-specific habitat. Pacific halibut undergo ontogenic shifts in habitat use, settling in shallow water as juveniles (Norcross et al., 1995; Abookire et al., 2001) and moving deeper with age (Best and Hardman, 1982; Hoag et al., 1997). Age-specific distribution and commercial catch rates have also been documented in U.S. west coast Dover sole (*Microstomus pacificus* [Jacobson et al., 2001]), and Piet et al. (1998) have suggested that flatfish partition with respect to gape size. Importantly, segregation by size could cause faster-growing individuals within each cohort to aggregate separately from slower-growing individuals, potentially generating skewed mean demographics depending on the relative distribution of capture effort to patch distribution.

Our ability to draw specific conclusions regarding sex-specific aggregation was limited by our inability to dissect all individuals, but sex-based structure was still detected. Pacific halibut exhibit sexually dimorphic growth (Gorchinsky, 1998; Clark et al., 1999) and even in the absence of true sex-specific differences in behavior, females likely predominate in legal-size aggregations owing to larger size-at-age (Clark, 2004); males, conversely, should be more abundant in patches of sublegal-size halibut. Sex-specific seasonal aggregation is also likely, given the species' documented seasonal redistribution and concentration at winter spawning grounds (St. Pierre, 1984; Loher and Blood, 2009; Seitz et al., 2011). Likewise, petrale sole (*Eopsetta jordani*; Hannah et al., 2002) and Kobe flounder (*Crossorhombus kobensis* [Moyer et al., 1985]) have been shown to exhibit seasonal aggregation for mating. In the case of Pacific halibut, analysis of behavioral data indicates that recent commercial fishing seasons have intersected the species' seasonal migratory period to a considerable degree (Loher, 2011), potentially allowing catch demography to differ during autumn and spring, relative to when summer survey data are collected. Additionally, there is evidence that Greenland

halibut (*Reinhardtius hippoglossoides*) may aggregate on the basis of sex in association with environmental factors, latitude, and depth (Gorchinsky, 1998).

In addition to the potential disparity between survey and commercial sex ratios, spatial aggregation may affect other indices, such as cohort-specific selectivity and abundance estimates. Longline catches may yield an imperfect reflection of assemblage structure simply owing to the nature of the gear. Once fish become hooked they preclude the capture of other fish, even if those arriving later are better competitors, a process that at high relative abundance can lead to "gear saturation." Although we may view longline catches as a snapshot of the underlying population, they are really an integration of potentially changing assemblage structure over soak-time. The influence of hook size and spacing, factors that do not vary in time and space, upon selectivity have received considerable attention (Skud and Hamley, 1978; Løkkeborg and Bjordal, 1992; Woll et al., 2001), whereas social interactions have received less. However, both laboratory (Stoner and Ottmar, 2004) and field (Løkkeborg et al., 1989) results have shown that hook occupancy patterns can be affected by behavioral interactions as well as by relative abundance. As such, the apparent selectivity of any particular demographic segment may vary depending upon the local density of competitors or upon the timing with which competing population segments arrive at the gear. Selectivity may vary in space and time even when underlying abundance of the target demographic remains relatively constant, or a single selectivity pattern may arise from a variety of different underlying population structures. With respect to abundance estimation, spatial stock structure may influence catchability where static surveys overlap mobile aggregations (*sensu* Dew and Austring, 2007). For halibut in the eastern Pacific, this could be relevant for the use of surveys to estimate abundance of prerecruit age classes, for which commercial CPUE is generally lacking, especially if the tendency to aggregate changes with age. Halibut distribution is highly spatially structured at young ages (Norcross et al., 1995), whereas use of a static survey design assumes relatively homogenous distributions of indexed ages.

Conclusion

In conclusion, analysis of Pacific halibut aggregation on a variety of spatial scales warrants more attention; in particular, on scales approaching those at which the survey and fishery are prosecuted, such as among survey stations, within the setting patterns of longline sets of commercial vessels, and among adjacent fishing grounds. In the meantime, methods that do not rely upon the assumption of demographic concordance between survey and commercial catches should be sought to verify the true sex composition of commercial landings.

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