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SETTLEMENT INDICES FOR BLUE CRAB MEGALOPAE IN THE YORK RIVER, VIRGINIA: TEMPORAL RELATIONSHIPS AND STATISTICAL EFFICIENCY

Karen S. Metcalf, Jacques van Montfrans, Romuald N. Lipcius and Robert J. Orth

ABSTRACT

The efficacy of artificial settlement substrates in quantifying relative rates of settlement of blue crab, *Callinectes sapidus*, postlarvae (megalopae) was examined. The technique has been widely used to assess settlement at local (Chesapeake Bay) and broad geographic scales (Atlantic and Gulf Coasts). This analysis examined differences in settlement between two configurations of substrates and two depths of deployment, in relation to lunar day, month, year and hours of flood tide occurring at night. Substrates were deployed daily for four years (1989–1992) during the settlement season (July–November) in the York River, Virginia. Settlement did not differ between substrate configurations (flat and cylindrical) deployed at the same location in the water column. Substrates deployed at the bottom of the water column had higher settlement than substrates at the surface, except during the last lunar month sampled (approximately November), when settlement was higher at the surface. There was a semilunar periodicity in settlement with high settlement following the new and full moon phases. Settlement varied annually and with lunar month. Statistical efficiency was achieved with a minimum of three or four replicate substrates. Cylindrical artificial settlement substrates are efficient, reliable and capable of detecting temporal patterns in settlement.

The importance of recruitment processes in the population dynamics of marine species with pelagic larval dispersal has been stressed in numerous recent studies (Cameron, 1986; Gaines and Roughgarden, 1987; Richards and Lindeman, 1987; Butman, 1987; Doherty and Fowler, 1994). Stochastic, physical processes have a dominant influence on transporting planktonic stages in these species over variable distances, but with behavioral modifications enabling non-passive distribution in some (Boehlert and Mundy, 1988). Eventually, those that survive to advanced larval stages encounter suitable nursery habitats where they settle, metamorphose into the adult form and potentially grow to a reproductive age.

Extreme fluctuations or cycles in population abundance over various temporal scales are often characteristic of fishery species such as the blue crab (Lipcius and Van Engel, 1990). These fluctuations may have complex ecological, economic and sociological consequences. Thus, understanding and anticipating such fluctuations remains a fundamental challenge for ecologists, fisheries scientists and resource managers alike.

The settling stage for some benthic or demersal marine (Connell, 1985; Gaines and Roughgarden, 1987; Roughgarden et al., 1985; Doherty and Fowler, 1994) and specifically, fisheries (Hjort, 1914; Phillips, 1986) species exhibits fidelity in recruit-stock relationships. For example, recruitment variability for reef-dwelling damselfish (*Pomacentrus muloccensis*) for a nine-year period and over spatial scales up to 70 kilometers accounted for 90% of the variability in year-class strength and population age structure (Doherty and Fowler, 1994). In addition, the Western Australian rock lobster (*Panulirus cygnus*) fishery can be accurately predicted 5 years in advance by quantifying postlarval and early juvenile stages settling on artificial substrates (Phillips, 1986; Phillips et al., 1994). Thus, for some species, the abundance of settlers directly projects the magnitude and composition of subsequent adult stages, and quantifying settlement provides a viable means of predicting and managing these stocks.

Quantifying the earliest life-history stage that will result in accurate predictions can yield the greatest lead time for forecasting year-class strength. Thus, developing techniques to determine abundance of advanced larvae, postlarvae or early juveniles at relevant temporal and spatial scales is requisite for such assessments of fisheries stocks, or for meaningful ecological research on post-settlement processes. Crustacean fisheries are amenable to developing indices of population abundance through quantitative estimates of settling stages (Witham et al., 1968; Phillips, 1972, 1986; Little and Milano, 1980; Morgan et al., 1982; Beninger et al., 1986). Quantifying settlement on artificial substrates at relevant temporal scales has also aided in identifying settlement patterns and examining the regulatory processes of settlement and recruitment dynamics in species such as the blue crab (Lipcius et al., 1990; Olmi et al., 1990; van Montfrans et al., 1990; Metcalf and Lipcius, 1992; Perry et al., 1995; Rabalais et al., 1995; Mense et al., 1995; van Montfrans et al., 1995).

The blue crab, an important commercial and ecological species may also be amenable to forecasts of year-class strength. Ovigerous females along the Western Atlantic, at the mouths of estuaries, release up to eight million larvae (zoeae) per individual (Van Engel, 1958; Prager et al., 1990). These larvae are subsequently transported to offshore coastal water for development through seven or eight stages (Provenzano et al., 1983; McConaugha et al., 1983; Epifanio et al., 1989). Next, metamorphosis occurs to the megalopal (postlarval) stage which eventually reinvades (i.e., recruitment) nursery habitats within an estuary (McConaugha et al., 1983; Epifanio et al., 1989). In Chesapeake Bay, megalopae settle predominantly in seagrass (*Zostera marina* and *Ruppia maritima*) beds, and also in other shallow-water areas (i.e., settlement), prior to metamorphosis into the first juvenile crab instar (Orth and van Montfrans, 1990). Because these reinvading megalopae represent survivors of a massive larval output (sensu Fritz et al., 1990), it is at the megalopal stage that understanding the importance of recruitment processes seems most feasible.

Flat artificial settlement substrates floating vertically at the water surface have been used since 1985 for quantifying the timing and magnitude of blue crab megalopal settlement in Chesapeake Bay (van Montfrans et al., 1990). Settlement on surface substrates was targeted since reinvading megalopae exhibit diel vertical migration and tidally-timed swimming behavior (Sulkin et al., 1980), which collectively result in a high abundance of megalopae in surface waters during nocturnal flood tides (Olmi, 1994; Mense and Wenner, 1989; Little and Epifanio, 1991). Fixed position, flat, near-surface (i.e., at a fixed location 1 m below mean low water) and bottom (i.e., 1 m above bottom) substrates were deployed in Charleston Harbor, South Carolina to examine diel settlement patterns of brachyurans, particularly the blue crabs (Boylan and Wenner, 1993). To standardize methodology for comparative purposes, these techniques were modified by adopting cylindrical substrates to accommodate additional sites with high current flow regimes throughout the Atlantic and Gulf coasts of North America (Rabalais et al., 1995; van Montfrans et al., 1995). Balanced internal weighting and flotation within cylindrical substrates assured a vertical orientation in the water column, irrespective of normal tidal flow direction or magnitude.

To date, quantitative differences in blue crab megalopal settlement as a function of substrate configuration (i.e., flat and cylindrical) and location of deployment (i.e., surface vs bottom) have not been determined. We believed it necessary to examine these relationships due to the widespread use of surface cylindrical sub-



Figure 1. Schematic of artificial settlement substrates. a. Flat substrate, b. Cylindrical substrate support blown up, c. "Hog's Hair" sleeve and rubber bands, d. Cylindrical substrate as deployed in the water column.

strates to quantify blue crab settlement. In addition, the statistical efficiency of these substrates has not been assessed. Thus, we compared settlement on the flat and cylindrical substrates deployed at the surface and cylindrical substrates deployed near the bottom of the water column at various temporal scales. We examined daily settlement of blue crab megalopae over the recruitment season (July–November) for 4 years as a function of substrate configuration (flat or cylindrical), number of substrates, location in the water column (surface or bottom), lunar day, month, year, and the hours of flood tide occurring during darkness. We also determined, for each substrate configuration, the number of replicate substrates necessary to minimize the variances in megalopal settlement.

METHODS

We utilized three substrate configuration/depth combinations: flat surface substrates, N = 6; cylindrical surface substrates, N = 4 (in 1992, 6 surface cylindrical substrates were sampled) and, cylindrical bottom substrates, N = 4. Artificial settlement substrates were constructed of "Hog's Hair" airconditioning filter material. Flat surface substrates (Fig. 1a) were constructed from single sheets of Hog's Hair (47 cm \times 39 cm, total surface area = 0.38 m²), held flat with a thin wood brace at the top and a weight (1 kg) at the bottom, and suspended vertically from floats within 10 cm of the water surface, perpendicular to the prevailing current (van Montfrans et al., 1990). Cylindrical surface and bottom substrates (Fig. 1b-d) were constructed of a PVC pipe cylinder (16.3 cm outside diameter, 37.5 cm length) surrounded by a Hog's Hair sleeve (total surface area = 0.26 m^2). Thus, flat substrates had 1.5 times more exposed surface area than cylindrical substrates. Each cylinder maintained a vertical position in the water column with a lower internal weight (1.5 kg) and upper internal float (Fig. 1b). Both configurations of surface substrates sampled the same portion of the water column at the water surface, whereas bottom substrates were suspended 10 cm above the sediment. All substrates were deployed from fixed locations along the length of a pier in the York River, a tributary of lower Chesapeake Bay, Virginia (37°14'N, 76°30'W), where water depth approximated 1.5 m at mean low water.

Substrates were deployed and retrieved between 0700 and 0900 h each morning. Flat substrates

were sampled with a long-handle dipnet (mesh size = 0.5×0.8 mm). Cylindrical substrates were lifted from the water column into a 19-liter bucket. Clean, air-dried substrates were then re-deployed. Substrates were rinsed with freshwater and associated fauna collected on a 0.5 mm sieve following standard procedures (van Montfrans et al., 1990). Surface and bottom cylindrical substrates were sampled from July through November, 1989–1992. Flat surface substrates were sampled from July through November, 1989–1991.

Statistical Analyses.—We determined the relationship between sample size and settlement variance (i.e., statistical precision of using four replicates of each substrate type to sample settlement), by calculating the standard deviations of the first two substrates of any type for each day and comparing these (using the correlation coefficient) to the standard deviation of the first three substrates. Then, the first three substrates were compared to the first four (up to four or six cylindrical or 6 flat substrates). Each data set (by year, depth of deployment and configuration of substrate) was randomly shuffled. These procedures were repeated 200 times to achieve a simulated sampling distribution. Statistical efficiency was attained when the standard deviation no longer decreased significantly upon increase of the sample size (i.e., addition of a substrate) and the correlation coefficient approached 1.0.

Settlement data were standardized by substrate surface area, and general linear models (GLM) were used to examine the statistical significance of year, lunar month, substrate configuration, depth of deployment, lunar day and hours of flood tide occurring at night. Two orthogonal analyses were conducted. The first encompassed the 3 years (1989-1991) when both substrate configurations were sampled at both depths, and examined differences by substrate configuration and depth of deployment. The second analysis encompassed 4 years (1989-1992) when both surface and bottom cylindrical substrates were sampled and compared. Data records were truncated (116 days per year) to include comparable lunar months for analysis. The lunar month encompassing 1 January of any given year was designated lunar month 1; thus, lunar month 8 was initiated by the new moon in late July or early August for the purpose of our analyses. Multiple comparisons were made using Ryan's O-Test (Einot and Gabriel, 1975). Lunar day (e.g., a semilunar cycle) was represented as a sinusoidal covariate, with a period of 14.75 days. The fit of this term to the settlement record was examined at various lags, with +4 days yielding the best fit. Hence, subsequent analyses used a lag of +4 days for the sinusoidal term. The duration (h) of flood tide occurring during darkness each night was also tested as a covariate (using both linear and quadratic terms) against the residuals of the multifactor analysis to determine the extent to which this covariate contributed to the variance. This measure was used because it reflected the amount of time megalopae were in the water column during their ingress into settlement habitats (Olmi, 1994).

RESULTS

The precision analyses indicated that four and sometimes three replicates minimized effort while reducing sample variance (Fig. 2). The correlation between the variances of consecutive sets of replicates approached 1.0 at three or four replicates (i.e., the correlation was greater than or equal to 0.90).

Overall, settlement of blue crab megalopae varied significantly with year, lunar month and depth of deployment, and with the covariate for lunar day. Results of these analyses will follow in factor order: significance of year, lunar month, lunar day, hours of nocturnal flood tide, and substrate location and configuration.

There was significant interannual variation in settlement for both data sets (4 years of surface and bottom substrates and 3 years of both substrate configurations and depths). Differences in annual mean settlement of megalopae did not vary by substrate configuration, but did vary by lunar month, probably due to seasonally varying pulses of settlement (Table 1). Data were therefore collapsed across months to eliminate the effect of these episodic peaks in order to summarize interannual differences in settlement (Fig. 3). The 1989–1992 data with cylindrical substrates at surface and bottom (GLM, F = 104.93, df = 3, P = 0.0001) revealed the same pattern with respect to year as those for 1989–1991 with both substrate configurations and depths (GLM, F = 305.87, df = 2, P = 0.0001). Settlement was significantly lower in 1989 (mean = 0.95 individuals per substrate unit surface area) than other years; significantly higher in 1990 (mean = 4.63 individuals per substrate unit surface area) than in other years; and did not differ significantly



Contrast between numbers of substrates

Figure 2. Mean correlation coefficients (\pm SE) from comparisons of standard deviations of number of megalopae per substrate for each number of replicates (N = 1, 2... 5 versus N + 1 replicates. Comparisons were made for 200 randomizations of the data sets (e.g., contrast 2 vs. 3 compares the standard deviations of 2 replicates vs. 3 replicates). Configurations with 4 replicates are combined across years in a single plot.

between 1991 (mean = 2.18 individuals per substrate unit surface area) and 1992 (mean = 2.39 individuals per substrate unit surface area) (Fig. 3).

Lunar month was a significant factor for all combinations of year and substrate type (Table 2). The magnitude of settlement varied between lunar months, but within years, the patterns were generally similar. Months with the highest settlement for any given year were high for all substrate types.

Lunar month	Surface flat	Surface cylindrical	Bottom cylindrical
8	F = 146.07 P = 0.0001	F = 72.09 P = 0.0001	F = 51.02 $P = 0.0001$
	90 91 89	90 92 91 89	90 92 91 89
9	$\overline{F} = \overline{7.42}$ P = 0.0007	$\overline{F = 9.63}$ $P = 0.0001$	$\overline{F} = 19.18 P = 0.0001$
	90 89 91	92 90 89 91	92 89 90 91
10	$\overline{F = 84.12}$ $P = 0.0001$	$\overline{F} = 56.80 \ P = 0.0001$	$\overline{F} = 98.53$ $P = 0.0001$
	90 91 89	90 91 89 92	<u>90 91 89 92</u>
11	$\overline{F = 38.31}$ $P = 0.0001$	$\overline{F} = 55.44$ $\overline{P} = 0.0001$	$\overline{F = 38.16}$ $\overline{P} = 0.0001$
	90 91 89	90 91 89 92	90 91 89 92

Table 1. Results of general linear models procedure for factor year (lunar month $8 \approx$ August, $9 \approx$ September, $10 \approx$ October, $11 \approx$ November; df = 2 or 3). Results of Ryan's Q multiple comparisons are shown; lines under more than 1 year are not significantly different.

The sinusoidal term reflecting semi-lunar periodicity in settlement was significant for 1989–1992 data with surface and bottom cylindrical substrates (GLM, F = 16.50, df = 1, P = 0.0001) and for data with both substrate configurations and depths during 1989–1991 (GLM, F = 12.29, df = 1, P = 0.0005) (Fig. 4). Settlement peaked during periods following the new and full moon (approximately 3–5 days). The covariates for hours of nocturnal flood tide (linear and quadratic terms) were both significant (except for the quadratic term in the analysis of both



Figure 3. Mean settlement (# individuals per substrate unit surface area + SE) by year collapsed across lunar months for each substrate configuration. Results of Ryan's Q-tests are represented by the horizontal bars; years under the same bar are not significantly different.

Year	Surface flat	Surface cylindrical	Bottom cylindrical
1989	F = 14.76 $P = 0.0001$	F = 4.95 $P = 0.0022$	F = 51.39 $P = 0.0001$
	<u>9 11 10 8</u>	<u>9 11 10</u> 8	<u>9 10 8 11</u>
1990	F = 28.30 $P = 0.0001$	F = 22.65 $P = 0.0001$	F = 29.62 $P = 0.0001$
	<u>8 10 11 9</u>	<u>8 10 11 9</u>	<u>8 10 9 11</u>
1991	F = 58.26 $P = 0.0001$	F = 19.87 $P = 0.0001$	F = 69.36 $P = 0.0001$
	10 11 8 9	<u>10 11 8 9</u>	<u>10 11 8 9</u>
1992		$\overline{F = 114.18}$ $P = 0.0001$	$\overline{F} = 85.22$ $P = 0.0001$
		<u>8 9 10 11</u>	<u>8 9 10 11</u>

Table 2. Results of general linear models procedure for factor lunar month ($8 \approx \text{August}$, $9 \approx \text{September}$, $10 \approx \text{October}$, $11 \approx \text{November}$; df = 3). Results of Ryan's Q multiple comparisons are shown; lines under more than 1 month are not significantly different.

substrate configurations and depths during 1989–1991, Table 3). The residuals of the GLM analysis, without the tidal covariate (hours of flood during darkness), regressed on the linear and quadratic covariates indicated that the contribution of the tidal terms to the overall model was small ($r^2 < 0.01$ for both data sets).

Settlement varied significantly with substrate depth of deployment for most lunar months during all years (Fig. 5). Settlement was significantly higher or not different on bottom than surface substrates during lunar month 8 (generally Au-



Figure 4. Mean settlement of blue crab megalopae (# individuals per substrate unit surface area + SD) by lunar day for all substrate configurations. Lunar day 1 and lunar day 14 or 15 are the new and full moon, respectively, a. 1989, b. 1990, c. 1991, d. 1992.

Data set	Linear term	Quadratic term
1989–1992 cylindrical sur- face and bottom	F = 23.66 df = 1 P = 0.001	F = 11.71 df = 1 P = 0.0006
1989–1991 both substrate types and depths	F = 76.01 df = 1 P = 0.0001	F = 1.99 df = 1 P = 0.1581

Table 3. Results of general linear models analysis for the covariate reflecting hours of nocturnal flood tide (both linear and quadratic terms)

gust) (GLM, 1989, F = 0.40, df = 2, P = 0.6730; 1990, F = 3.20, df = 2, P = 0.0418; 1991, F = 0.74, df = 2, P = 0.4784; 1992, F = 0.02, df = 2, P = 0.8939) and during lunar month 9 (GLM, 1989, F = 37.44, df = 2, P = 0.0001; 1990, F = 17.95, df = 2, P = 0.0001; 1991, F = 1.91, df = 2, P = 0.1499; 1992, F = 24.44, df = 2, P = 0.0001). Settlement during lunar month 10 did not differ significantly between substrate depth or configuration (GLM, 1989, F = 0.67, df = 2, P = 0.5127; 1990, F = 1.59, df = 2, P = 0.2057; 1992, F = 0.10, df = 2, P = 0.7466), except in 1991, when settlement on bottom substrates was



Figure 5. Mean settlement (# individuals per substrate unit surface area \pm SE) by substrate configuration and depth for each lunar month. Substrate types are abbreviated: SF, surface flat substrate, SC, surface cylindrical substrate, BC, bottom cylindrical substrate. Horizontal lines indicate the results of Ryan's Q multiple comparison test results. Substrate types under the same bar are not significantly different.

Year	Surface flat vs. Cylindrical	Cylindrical surface vs. Bottom	Flat surface vs. Cylindrical bottom
1989	0.817	0.334	0.355
1990	0.756	0.471	0.592
1991	0.876	0.621	0.563
1 992		0.647	

Table 4. Correlation coefficient matrix for each combination of year and substrate type. All combinations are correlated significantly (P < 0.05, N = 116).

higher than on surface substrates (GLM, F = 25.29, df = 2, P = 0.0001). Settlement patterns changed with respect to substrate depth during lunar month 11. Settlement magnitude on the two surface substrate types (i.e., flat vs. cylindrical) did not differ, but was significantly higher than that on bottom substrates (GLM, 1989, F = 7.62, df = 2, P = 0.0006, 1990, F = 11.01, df = 2, P = 0.0001, 1991, F = 5.97, df = 2, P = 0.0028) except in 1992 (GLM, F = 0.42, df = 1, P = 0.5155) when there was no difference.

Settlement on the flat surface substrates correlated significantly with settlement on the cylindrical surface substrates at a lag of 0 days (Table 4). Similarly, daily settlement rates on both flat and cylindrical surface substrates correlated directly (no time lag) and significantly with settlement on bottom substrates (Table 4). Settlement on the two surface substrate configurations were highly correlated, with no correlation coefficient less than 0.75. Settlement on the two surface substrates also correlated with bottom substrates, but not as strongly. The correlation coefficients between surface and bottom substrates ranged from 0.33 to 0.65.

DISCUSSION

The observed high variability in settlement by blue crab megalopae is characteristic of many fisheries species, and challenges ecologists and managers in attempts to understand population fluctuations. Techniques that measure annual variability in settlement or recruitment, such as artificial settlement substrates, may be useful in examining year class strength by cross-correlations with the fishable stock. For instance, Lipcius and Van Engel (1990) examined juvenile and adult indices for the blue crab in the York River, Virginia, and found a significant cross-correlation between fisheries landings and the indices of abundance. If settlement variability is quantified at appropriate scales, this technique might provide a reliable measure of blue crab abundance 2 years hence. If this relationship does not hold, then settlement timing and magnitude can be useful in examining density-dependent processes that cloud recruit-stock relationships.

Although settlement magnitude of blue crab postlarvae was episodic on a daily scale, there were detectable temporal patterns on a lunar scale. The timing of settlement by blue crab megalopae was temporally predictable and covaried significantly with semilunar and tidal functions (hours of flood tide occurring at night). The tidal and semilunar functions were likely related because tidal timing covaries with lunar phase (i.e., a higher proportion of each flood tide occurs at night approximately 4 days after the new or full moon and tidal flow increases during spring tides associated with new and full moon). Thus, both factors may have influenced settlement similarly.

The semi-lunar factor was reflected in the occurrence of significant settlement peaks approximately 4 days following the new and full moon. These findings are similar to earlier studies in the York River which described a semilunar periodicity in blue crab settlement (van Montfrans et al., 1990). Stronger new moon peaks of settlement during some years of our study than those observed during 3 earlier years attest further to the annual variability of settlement patterns. Settlement in the York River had a strong semilunar component with generally higher settlement associated with periods after the new or full moon. Similarly, settlement of blue crabs in Charleston Harbor, South Carolina was greatest during the fourth quarter (Boylan and Wenner, 1993). These locations differ in their distance from the source of postlarvae. The site sampled at Charleston Harbor is located near the mouth of the estuary, while the site in the York River is 50 km from the mouth of Chesapeake Bay. This may have resulted in the delay in settlement at the upestuary site. This timing is likely a result of the vertical migration behavior of megalopae, which are in the water column on nighttime flood tides and the increased transport capability afforded by spring tides. In both locations, however, the magnitude of settlement during any given lunar period or month varied annually.

Settlement differed depending on lunar month and substrate location. For the first 3 lunar months (generally lunar months 8–10), settlement was generally higher on the bottom substrates. For the last lunar month sampled (11), settlement was consistently higher on the surface than bottom substrates. A plausible explanation is that megalopae entering the York River during lunar month 11 and experiencing cooler water temperatures, may be less advanced in the molt cycle than megalopae which immigrate earlier in the year, and, therefore, less likely to be near the bottom (Lipcius et al., 1990; Metcalf and Lipcius, 1992).

Settlement timing can have important ecological and management implications for blue crab populations. Individuals which settle early in the recruitment season (July–September) experience warm water temperatures and, therefore, may exhibit faster growth than those settling later in the season (October–November). However, survival could be higher later in the recruitment season with the exodus of major fish predators from shallow nursery habitats concurrent with decreasing temperature. From a fisheries perspective, early settlers will likely enter the fished segment of the population sooner than those settling later due to increased growth potential. However, the abundance of these early settlers could be negatively impacted through more intense density-dependent predation than the abundance of those settling later in the recruitment season, during colder months (Metcalf et al., unpublished data). Settlement data could be used to examine such important ecological relationships and their implications for population dynamics and fisheries management.

Differences in settlement between months were related to the episodic nature of blue crab settlement. Within a given year, however, monthly differences in the magnitude of settlement exhibited similar patterns, regardless of substrate type. Settlement on flat and cylindrical surface substrates did not differ significantly when standardized for surface area. Cross-correlation analyses indicated that patterns of settlement were the same for all of the substrate types. Only the magnitude of settlement differed between substrate configurations and depth, although the two surface types were more closely correlated than either were with bottom substrates. The results of the efficiency analysis indicated that four, or sometimes three, replicate substrates were statistically sufficient to characterize variability in settlement, emphasizing the simplicity of this technique for quantifying relative rates of settlement of blue crab postlarvae.

Hence, artificial settlement substrates are a useful tool for quantifying settlement of blue crab postlarvae and subsequently, projecting juvenile abundance and fishery harvest. This method offers a practical and inexpensive solution to the problem of assessing differences in the magnitude of settlement across wide geographic areas, and potentially for predicting commercial landings.

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