Growth and Reproduction of the Tidepool Sculpin
Oligocottus maculosus

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Abstract   Growth and reproduction of tidepool sculpins (*Oligocottus maculosus*) from three sites in Puget Sound, Washington State, USA were characterized.   One site was a sandy, gently sloping beach, the second was an exposed rock headland with minimal algal cover, and the third was an exposed rock headland with numerous tidepools containing abundant algal cover.   Length-weight relationships for sculpins did not differ significantly between sexes within sites.   Population age structure, growth rate and recruitment varied among the three study sites using data pooled across both sexes.   Young-of-the-year sculpins comprised 91 % of the population at the exposed headland site with minimal algal cover but only 6 % at the headland with abundant algal cover.   Selective predation by great blue herons (*Ardea herodias*) upon tidepool sculpins larger than 45 mm total length assisted in the maintainance of these age structures.   A maximum gonadosomatic index of 28.5 was calculated; this index correlated poorly with either age, length or somatic weight.   Diameters of unshed ova from preserved tidepool sculpins sampled prior to spawning fell into three classes.   Comparison of the mean egg size of each mode and the number of modes present in preserved sculpins with similar data from tidepool sculpins that spawned in the laboratory suggested that spawning occurred twice yearly from at least January through August.

The tidepool sculpin, *Oligocottus maculosus* Girard, is a small cottid inhabiting rocky intertidal areas along the northeast Pacific coast (Hart, 1973).   Although occasionally found in shallow eelgrass habitats (Read, 1968), this sculpin typically dwells in tidepools where broad habitat, temperature, salinity and food requirements (Nakamura, 1976a, b; Green, 1971c) often make it the most abundant fish species (Moring, 1976).

Many studies on the tidepool sculpin focus upon behaviour, for instance, Eastman's (1962) pioneering research on homing ability following displacement.   Homing occurs in 60–80% of 50–90 mm individuals tested (Green, 1971a), depends more upon olfaction than vision (Khoo, 1974), is most successful in age II fishes (Craik, 1981), and takes place relatively rapidly (generally within two tidal periods; Green, 1971a).   Green (1971b) showed that rhythmicity of the tidepool sculpin's locomotor activity correlated with tidal cycles; activity decreased greatly during the low tidal phase.

Despite such advances, few data describe the life history and biology of the tidepool sculpin.   Nakamura (1971) showed that tidepool sculpins are general and opportunistic feeders while Atkinson (1939) evaluated the relationship between length and weight and proposed that the fish was a multiple spawner.   The purpose of our research was to examine the life history of the tidepool sculpin at three diverse sites for comparison with historic data, particularly Atkinson's, and to evaluate the environmental influence on growth rate, fecundity, population age and size structure.   Knowledge of variability within these parameters is essential if the ecological bases for and implications of experimental results (such as displacement) are to be understood.

Methods and materials

Three field sites in Puget Sound, Washington, USA, were sampled (Fig. 1).   Alki Point, Seattle, Washington is predominantly a gently sloping sand beach containing small shallow tidepools with little algal cover and minimal rock structure.   Green Point, Anacortes, is an exposed rock headland with a very steep slope, small tidepools, and minimal algal cover.   Tongue Point, near Port Angeles, is an exposed headland of intermediate slope with many tidepools of varying depths that contain extensive algal and rock cover.

On 5 January 1979 tidepools at Alki Point were

sampled with handnets at low tide. All visible sculpins were collected. Specimens were held briefly in aquaria, sacrificed, and frozen. Two weeks later these specimens were thawed, weighed (± 0.01 g) using the light blotting technique (Parker, 1963) and their total (TL) and standard lengths (SL) measured (± 0.5 mm). Neither freezing nor five day formalin preservation appreciably altered the mean total length, standard length or wet weight (n=48). Mean changes caused by freezing were -0.08%, -0.02% and 0.28%, respectively. Mean changes caused by formalin preservation were -0.04%, -0.05% and -0.05%, respectively. Ovaries were removed, weighed, and placed in individual vials containing 7% formalin. On 3 February 1979 live sculpins were again collected from Alki Point, but these sculpins were held in aquaria in 12°C recirculating seawater, fed grated English sole (*Parophrys vetulus*), and allowed to spawn. Immediately after spawning, the sculpins were sacrificed, preserved and examined as before. Tidepools at Alki Point were visited again on 14 March and 2 August 1979 to search for ripe females.

On 5 August 1979 one infralittoral and two midlittoral tidepools at Tongue Point were sampled with quinaldine after all rocks were removed. Tidepools at Tongue Point were again visited on 4 September 1979 to search for ripe females; no other sculpins were kept.

On 10 August 1979 tidepools were sampled at Green Point employing the same procedures used at Tongue Point.

Paired ovaries from 104 individual sculpins (52 from Alki Point, 48 from Tongue Point, and 4 from Green Point) were broken up and ova examined in water under a dissecting microscope equipped with a calibrated ocular micrometer. All oocytes (except those less than 0.10 mm which could not be consistently removed from the stroma without damage) were counted and diameters measured (± 0.01). Similar examinations were conducted using eggs and ovaries from sculpins that had spawned in the laboratory (n=2). Total annual fecundity of each female was defined as the number of albuminous ova present prior to spawning. Ova diameters from individual fish were highly variable depending on the state of maturity of the fish; hence, spawning modes were characterised as statistically discrete
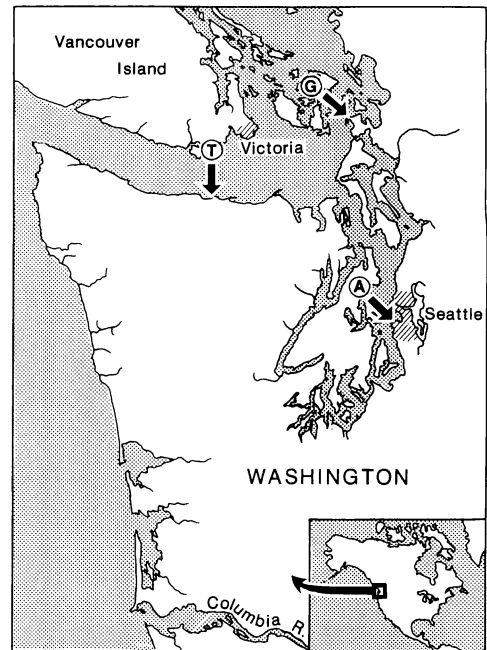

Fig. 1. Location of the study sites. A, Alki Point, Seattle, Washington; G, Green Point, near Anacortes, Washington; T, Tongue Point, near Port Angeles, Washington.

size distributions (Cassie, 1954, Harding, 1949) rather than particular ova diameters.

Age estimates were obtained by both length and weight frequency analysis and verified by reading growth rings on otoliths (n=29; Jearld, 1983; Bagenal and Tesch, 1978) and vertebral centra (n=11; Menon, 1950). The total length to weight relationship was calculated after $\log_{10}$ transformation of both variables. The ELEFAN1 computer program (Pauly and David, 1980) was used to calculate length-frequency-based parameters (L_∞=theoretical maximum length, K=growth coefficient, D=correction for mean environmental temperature, ESP/ASP ratio=data variance ratio, winter point=time of coldest part of the winter on an annual scale from zero to one) for the generalized von Bertalanffy growth formula (Pauly 1981):

$$L_t = L_\infty [1 - e^{-KD(t-t_0)}]^{1/D}.$$

On 4–7 and 28 August 1979, predation by the great blue heron (*Ardea herodias*) on tidepool sculpins was observed from cover at Tongue Point during low tide. Binoculars allowed iden-
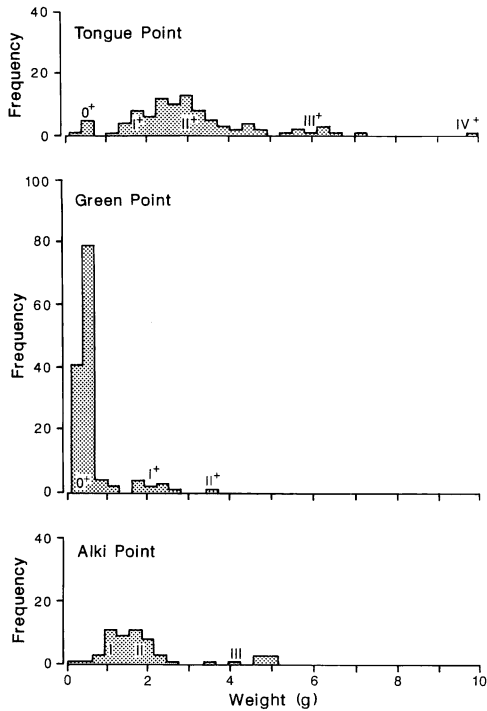
Fig. 2. Weight frequency distribution of tidepool sculpins, *Oligocottus maculosus*, from Tongue Point (5 August 1979), Green Point (10 August 1979) and Alki Point (5 January 1979).

tification of prey, timing of foraging and estimation of the length of captured sculpins by comparison with heron bill length.

Results

The relationship of standard length to total length was: SL=0.813 (TLmm). This relationship did not vary with sex, size (36.5–72 mm TL) or sampling locality.

The length-weight regression for female Alki Point tidepool sculpins in ripe spawning condition was significantly different from that of males (s= slope, i=intercept, Z_s=2.33, P<0.05, Z_i=−2.08, P<0.05, df=52). However, when the weight of the unspawned ovaries was subtracted from the total weight of each female to simulate non-breeding condition, no significant difference existed between the slope and intercept of the regressions for each sex (Z_s=1.28, Z_i=−1.27).

Similarly, no significant differences existed between the slope and intercept of the length-
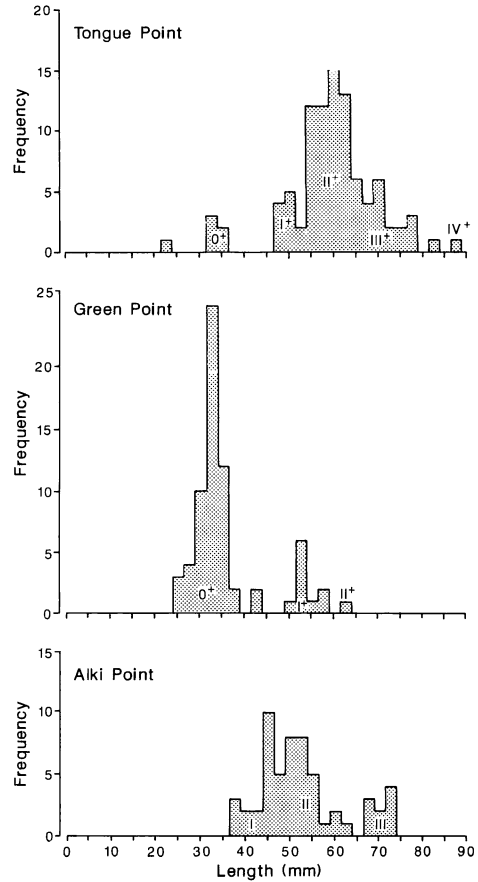

Fig. 3. Length frequency distribution of tidepool sculpins from Tongue Point (5 August 1979), Green Point (10 August 1979) and Alki Point (5 January 1979).

weight regressions for the male and female sculpins collected after the peak spawning period at Green Point (T_s=0.036, T_i=0.033) or Tongue Point (Z_s=0.20, Z_i=−0.37). After pooling across sexes, significant differences were not found between sites (using the corrected Alki Point female data; Alki X Green Point, Z_s=−0.69, Z_i=0.77; Alki X Tongue Point, Z_s=−0.58, Z_i=0.49; Green X Tongue Point, Z_s=0.15, Z_i=−0.39). Therefore, the pooled length-weight regression for all 256 Puget Sound tidepool sculpins sampled was: Ln (W)=−12.1+3.23 (Ln (TL)) where W=body weight in g.

The ages of mature sculpins (ages I, II and III) were most easily estimated by weight-frequency analysis (Fig. 2), but the ages of young-of-year (YOTY) sculpins were more easily determined
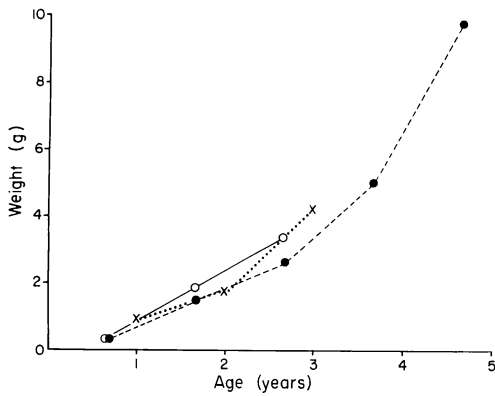
Fig. 4. The age-weight relationship for tidepool sculpins from three sites in Puget Sound. Data for each location were pooled across sexes. The crosses indicate Alki Point specimens, the solid circles Tongue Point fish and the open circles Green Point sculpins.

using length-frequency analysis (Fig. 3). Length-frequency and weight-frequency age estimates agreed in 96% of cases. All weight-frequency-derived age estimates agreed with age estimates derived from otolith and vertebral growth data; however, in one case (5%) length-frequency analysis disagreed with both otolith and vertebral age estimates. The oldest age estimated for any sculpin sampled during this study was IV+.

Population age structures constructed using weight-frequency estimates varied greatly between sites. August samples from Green Point indicated that YOTY fish made up 91% of the total tidepool sculpin population (8% age I+, 1% age II+) whereas concurrent samples from Tongue Point contained only 6% YOTY fish (23% age I+, 61% age II+, 15% age III+ and 1% age IV+). The growth rate of sculpins from each of the three sites also differed considerably (Fig. 4). Growth rate was inversely proportional to density (i. e., Green Point fish grew fastest, Tongue Point fish grew slowest but attained the largest size, and Alki Point sculpins had an intermediate growth rate).

The gonadosomatic index (GSI), where GSI = 100 (gonad weight/total weight), of female sculpins captured on 5 January 1979 at Alki Point was poorly correlated with age ($r^2 = 0.56$), length ($r^2 = 0.51$) or somatic weight ($r^2 = 0.42$), despite sampling just prior to the peak spawning period. GSI varied greatly between individual females at this
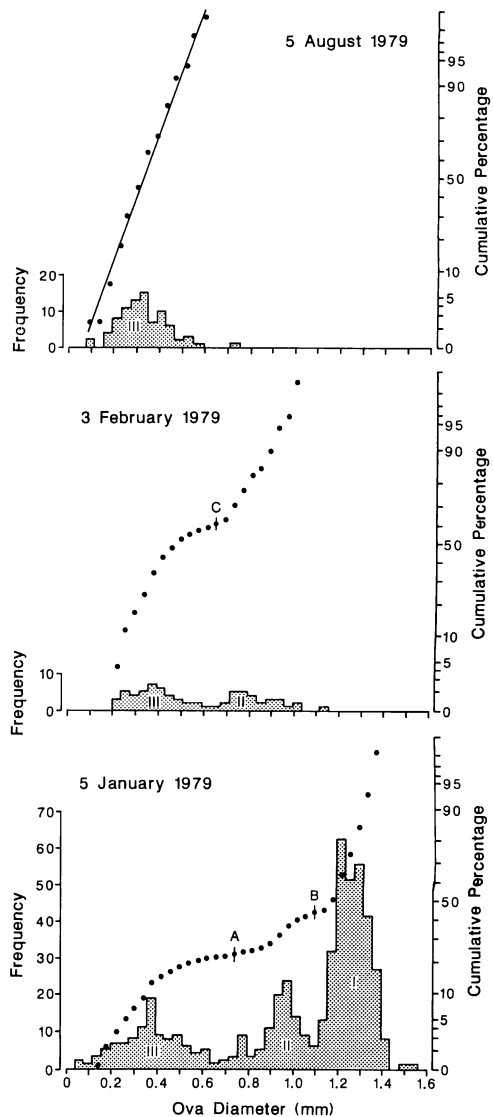

Fig. 5. Ova diameter frequency distribution for tidepool sculpins from Alki Point. Cumulative percent probabilities are plotted relative to the right axis with inflection points A, B, and C clearly visible. Top panel: Age II, 2.19 g sculpin collected on 5 January 1979 (prior to spawning). Middle: Age I, 2.09 g sculpin collected on 3 February 1979 (after spawning in the laboratory). Bottom: Age I+, 1.89 g sculpin collected at Tongue Point on 5 August 1979 (after completion of wild spawning).

time (n = 28, range: 8.3–28), but the diameter of oocytes in the largest mode (one, see below)

remained remarkably constant (range of means: 1.20-1.29 mm).

Alki Point sculpins collected on 5 January contained eggs distributed in three modes (Fig. 5) as confirmed by obvious inflection points in the cumulative percent probability plot.

Mode three eggs were present in all females captured (Fig. 5) and were assumed to be un-differentiated oocytes. Besides being much smaller, eggs in mode three were distinct in their white coloration (vs. green) and irregular (vs. round) shape. By August, all but one sculpin contained only mode three eggs.

Mode two eggs represented the second spawning of the sculpin in one year. The presence of only two size modes in the ova of females captured on or after 14 March and only one mode after 4 September supported this hypothesis. For example, only two size modes were present in the (non-atresial) ova from the one ripe sclpin col-lected at Tongue Point on 5 August 1979. This third mode represented undifferentiated oocytes while the second consisted of large (mean=1.21 mm) albuminous eggs yet to be spawned. Non-oviferous sculpins collected concurrently con-tained only undifferentiated mode three oocytes.

Mode one eggs represented the first spawning of the sculpin in a year. All female sculpins captured on or after 14 March 1979 lacked mode one ova. The mean size of mode one ova found in Alki Point females in January matched the mean size of fertile eggs laid in the laboratory (1.22±0.034 mm; range 1.08-1.32 mm, n=2 spawnings) by recently captured sculpins. Mode one eggs were absent from the ovaries of sculpins following laboratory spawning (Fig. 5), thus, in this instance, females laid all mature eggs at one time. Mode two and one eggs were bright green. Laboratory spawned eggs were also green and were laid in a single cluster on a hard surface.

Annual fecundity (F) observed in unspawned female sculpins from Alki Point was a linear function of both total length (r^2=0.96) and weight (r^2=0.95): F=−9.47+171(W); F=−8.25 +21.9(TLmm). Mode two (second spawnings) ova represented only 9.0-16% (n=4) of the total annual fecundity for age I Alki Point females, but 23-40% (n=3) for the larger age II females.

Immediately prior to the peak spawning period (mid-February in 1979), all female, age I tidepool sculpins contained mature ova. Hence, sexual

maturity was attained by 12 months of age under existing conditions. The time of male maturity could not be unambiguously determined. Mean annual fecundity (number of eggs laid during one breeding season) for Alki Point female sculpins was approximately 103 for age I sculpins, 401 for age II sculpins, and 699 for age III sculpins. Based on ovarian contents, the first spawning of the season always contained a greater number of eggs than did the second.

Five heron predation events on tidepool sculpins were observed; no other fish species were captured. Foraging times per prey item were 24, 15, 8, 21 and 26 minutes (mean=19 minutes) with herons arriving, capturing a single fish and leaving in each instance. All captured tidepool sculpins were estimated to be at least 45 mm TL.

Discussion

Within the Puget Sound region, we did not detect significant differences between growth patterns (as indicated by their length-weight relationship) displayed by tidepool sculpins collected from different sites. Hence, racial differences in growth pattern would not confound studies using specimens from different locations within this region. Size therefore is a valid indicator of environmental response.

The length-weight regression calculated for Puget Sound tidepool sculpins during this study was similar to that calculated by Atkinson (1939). Strict quantitative comparisons were not possible however, as the Atkinson study did not employ quantitative regression procedures. Our Alki Point length-frequency data in 1979 appeared indistinguishable from those of Atkinson; pooling the two data sets did not alter L_∞ and longevity values (longevity=3.85, K=0.85, K=0.35, D=1, winter point=0.1, ESP/ASP ratio=0.801) calculated using ELEFAN. Therefore, local population characteristics appear to be stable over time (i. e., 40 years) and the ELEFAN parameters from Atkinson's work apply equally well to the current Alki Point population. Thus, the growth pattern expressed by tidepool sculpins with the Puget Sound region appears to be broadly stable over both space and time.

Apparent differences in growth rate between Alaska and Puget Sound sculpin populations were evaluated. The most likely growth pattern

(based on differences in length-frequency data from at least two samples per year) was calculated using ELEFAN. Since the accuracy of this program is not biased by the magnitudes of absolute abundances, we interpolated length-frequency data from Atkinson's (1939) figures 4 and 5. L_∞ was estimated to be 96 mm TL for tidepool sculpins from Alki Point (longevity=3.85, K=0.35, D=1, winter point=0.1, ESP/ASP ratio=0.875), but was only 85 mm TL for Alaskan sculpins (longevity=3.48, K=0.5, D=1, winter point=0.1, ESP/ASP ratio=0.827). Without more information about the sampling site for Atkinson's Alaskan sculpins, predicting why his L_∞ value was considerably less than for Puget Sound fish is difficult.

Significant difference in recruitment were evident between the three Puget Sound tidepool sculpin populations sampled. Tongue Point had the most dense population but few recruits, whereas the sparse Green Point population had large numbers of YOTY. Apparent restricted larval movement alone (Marliave, 1986) would predict the exact opposite pattern to occur with the most recruits resulting from the largest parental stock. Grossman and DeVlaming (1984) suggested that productivity cycles govern recruitment success in the congeneric fluffy sculpin (*Oligocottus snyderi*). Our data and observations suggest an inverse density dependant recruitment pattern for this tidepool sculpin. Cannibalism (Nakamura, 1971) and competition for food between fry and adults could also produce similar effects.

Gibson (1982) implied that physical factors such as temperature and wave shock play roles in determining sculpin population density. At these three Puget Sound sites, wave exposure and temperature regimes were qualitatively similar. However, another factor, pool "quality" (i. e., structure and algal growth) differed considerably among the three sites. The fewest recruits were found at the site containing pools with extensive algal and rock cover whereas the largest number of recruits occurred in small tidepools containing minimal algal cover in the exposed rock headland. Since most prey items in the diets of tidepool sculpins were of benthic origin (Nakamura, 1970, 1971), we believe the greater benthic structure enhances food abundance. This increased food supply supported the higher population density observed at Tongue Point, however, size-at-age

was lowest here (Fig. 4) which may indicate competition for food between resident sculpins. Increased algal and rock cover probably also provided more available territories.

While Khoo (1974) dismissed predation as a regulator of tidepool sculpin populations, our observations of the great blue heron showed these birds to be very efficient at catching sculpins 45 mm TL and larger. Tidepool sculpins represented at least 95% of the cottids present in tidepools at these sites. Capture of YOTY-size fish was never observed. Hence, size selective predation by birds may partially explain the low percentages of older sculpins. The predominance of YOTY fish at Green Point (91% age 0) which lacked protective cover also supports this hypothesis. Similar avian predation is known to effect the local population structure of mosquitofish (*Gambusia affinis*; Britton and Moser, 1982).

Large specimens (75+mm TL) are occasionally captured in habitats other than tidepools (Read, 1968). Homing success decreased in larger fish (Craik, 1981), perhaps indicating diminished territoriality. Since young sculpins do not migrate long distances (Moring, 1976, Craik, 1981), dispersal of these large adults could facilitate recolonization, genetic exchange and feeding.

Although not statistically significant, the mean weights and lengths of tidepool sculpins collected at all three sites were consistently smaller in the higher tidepools. Young-of-the-year sculpins were considerably more abundant in the highest pools. This trend may suggest emigration into lower pools as size increases, but could also be caused by greater size selective predation in the upper pools. Green (1971c) showed that activity in tidepool sculpins was curtailed during the exposed (low tide) period; thus, increasing size may force sculpins into lower pools to seek larger prey and increase available foraging time to meet increased metabolic demands.

All tidepool sculpin eggs observed during this study were green. Green egg coloration also occurred in sculpin eggs laid by females which had been held in the laboratory for 25 days during which primary plant pigment sources had been absent from the diet. Egg coloration is associated with the yolk (Stein, 1973); hence, the white colour (as opposed to green) of mode one eggs probably implied low concentrations of yolk in these undifferentiated oocytes. Presumably the colour of

the yolk may stem from biliverdin pigments present in the diet of the fish, as occurs in *Clinocottus analis*, another shallow water cottid (Fang, 1986). Qualitative analysis of tidepool sculpin stomachs from spawning fish collected at Alki Point showed that the green alga, *Ulva*, was a common dietary component. Interestingly, Atkinson (1937) described freshly deposited Alki Point tidepool sculpin eggs to be blood red. Hence, a shift from predominantly red to green algae may have occurred at Alki Beach during the past 50 years, although corroborative historical data have not been uncovered.

Atkinson (1939) suggested that tidepool sculpins were multiple spawners. Our data specifically indicate that Puget Sound tidepool sculpins spawn twice yearly. No evidence was found to suggest fractional spawning. Laboratory data clearly demonstrated that mode one eggs are spawned first while the absence of mode two eggs from all but one female collected at Tongue Point in August demonstrated that eggs from mode two were spawned during the same season as the mode one eggs. The number of eggs in the first spawning may be limited by the internal volume available for ovary formation, as maximum ovarian volume (28%, assuming similar ovarian and somatic densities) was similar to the maximum stomach content volume (20%) observed.

Ripe tidepool sculpins were readily collected in the Puget Sound region from January through April, with few reproductive individuals occurring thereafter. Our data extend the spawning period for tidepool sculpins as reported by Atkinson (1939). Since spent sculpins were collected in early January, spawning probably begins in late December. Two of thirty (6.7%) female sculpins collected at Alki Point on 5 January 1979 had already spawned. While one ripe sculpin was collected in August, the percentage of ripe sculpins occurring during this month (2.3%) was quite low.

Qualitative observations during early January 1983 and 1985 at Green Point and Tongue Point indicated that the initial spawning period involved most members of the sculpin population, was highly synchronous, spanned a three or four week period, and occurred simultaneously throughout the Puget Sound region. The second spawning was asynchronous and extended over a six month period. Grossman and DeVlaming (1984) ob-

served a similar pattern in the fluffy sculpin *Oligocottus snyderi*. Since the majority of each female's reproductive effort, in terms of ova, was directed into the first reproductive period, greater relative recruitment from this spawning would be hypothesized. Wohlfarth and Moav (1970) showed that carp fry hatched one day later than competitors displayed considerably reduced survival and growth rates. These data, if applicable, would suggest greater recruitment from earlier spawnings and selection towards higher initial reproductive expenditures. Smaller secondary spawnings would be favoured (relative to no second spawning) if even minor recruitment occurred.

In summary, we concluded that tidepool quality and predation play significant roles in determining sculpin population structure and density. We hypothesized that food availability (which is directly influenced by the type of substrate and algal cover present in the tidepool) also plays a significant role. Each of these three factors differed among the three Puget Sound sites studied resulting in differing growth rates and population structures producing what might initially appear to be discrete tidepool sculpin populations. However, relative to length-weight and fecundity analyses, the sculpins functionally represent a single stock with length and growth under environmental control. Because each of these three factors (tidepool quality, predation, and food abundance) partially confounds another of the factors (i. e., predation depends to some degree upon algal cover), to obtain strict quantitative estimates of the contribution made by each factor will require further study.

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ブチカジカの生長と繁殖

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　米国ワシントン州のピュージェット海峡内の環境条件が違う3地域において，ブチカジカ *Oligocottus maculosus* の生長・繁殖特性を調べた．体長・体重関係については各地域ともに性差は認められなかった．両性を区別しない試料では個体群の年令組成，生長率および加入量に3地域間で相異がみられた．例えば，当才魚の割合は地域間で 6% から 91% の変異を示した．また，オオアオサギ *Ardea herodias* による全長 45 mm 以上の個体に対する選択捕食が，個体群の年令組成維持に関係していた．生殖腺指数（最大 28.5）と年令，体長，体重との間には明瞭な関係は見出せなかった．卵巣内卵径組成には3つのモードが識別された．これと実験室内での産卵状況とから，本種の産卵は少なくとも1月から8月までの間に年2回行なわれることが示唆された．