Density and production of *Clinocottus globiceps* and *Oligocottus maculosus* (Cottidae) in tidepools at Helby Island, British Columbia

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ABSTRACT: Density and production of 2 dominant tidepool resident species, *Clinocottus globiceps* and *Oligocottus maculosus*, were estimated over a 2 yr period at Helby Island, British Columbia, Canada. Mean densities of *O. maculosus* fluctuated considerably with 2.5 and 13.7 fish m^{-2} of tidepool areas reported for the first and second year respectively. Density estimates for *C. globiceps* were 1.9 and 2.5 fish m^{-2} during the same period. Production was estimated by instantaneous growth rate method. Annual production estimates for *O. maculosus* were 1.8 g m^{-2} yr^{-1} in the first year and 11.0 g m^{-2} yr^{-1} in the second year, and corresponding values for *C. globiceps* were 8.1 and 7.0 g m^{-2} yr^{-1} respectively. Production reflected the distribution pattern of the 2 species, i.e. higher production was observed at the upper intertidal pools for *O. maculosus* and at the lower pools for *C. globiceps*. The relationships between physical characteristics of tidepools and production of the 2 species are given. None of the physical variables examined was a significant predictor of production.

INTRODUCTION

Resident tidepool fishes have short home ranges (Gibson 1967, Richkus 1978, Grossman 1982) and some, notably *Oligocottus maculosus* and *Clinocottus globiceps* (Cottidae), exhibit strong homing behaviour (Green 1971a, 1973). Factors that influence vertical distribution of *O. maculosus* were investigated by Nakamura (1976a, b), whilst Green (1971a, b, 1973) has presented data on movement, distribution patterns and homing behaviour of *O. maculosus* and *C. globiceps* on the west coast of Vancouver Island, Canada. Moring (1976) studied population size of *O. maculosus* at a site in California, USA. Despite the ecological significance of dominant resident tidepool cottids, there is very scanty documentation of production estimates of individual species or an entire fish assemblage in tidepool environments. For example, only Bennett (1984) has reported on the energy budget and production of *Clinus superciliosus*, a tidepool resident of the south-western coast of South Africa. Bennett & Griffiths (1984) gave quantitative estimates (biomass) of an entire fish taxocene in the intertidal rocky pools on the Cape Peninsula, South Africa.

The objective of this study was to evaluate production dynamics of *Clinocottus globiceps* in comparison with the widely distributed *Oligocottus maculosus*. The term 'fish production' as used in this paper and by many authors (e.g. Ricker 1946, Allen 1951, Weatherley & Gill 1987) is defined in the sense of Ivlev (1945) as total weight of body tissue produced by a population of fish during a given interval of time, including growth by fish that died during the time interval. Information on production was combined with data on intertidal distributions of *C. globiceps* and *O. maculosus* to examine the relative importance of spatial (zonal) variability in production dynamics. This study focused on: (1) estimating and comparing densities and production of *C. globiceps* and *O. maculosus* by age group and by the populations as a whole, and (2) evaluating the influence of physical characteristics of tidepools (e.g. depth, perimeter and surface area) and population variables (e.g. growth and biomass) on production of these 2 species.

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MATERIALS AND METHODS

The study site is on a series of rocky tidepools on a rocky shelf stretching from the northeastern to northwestern beach (48° 51' N, 125° 10' W) at Helby Island on the west coast of Vancouver Island, British Columbia, Canada. The area is typical of open to semi-protected rocky intertidal habitats. The substratum consists mainly of boulders and cobblestones although several pools have patches of sandy bottom.

A total of 20 previously established bench marks in the intertidal zone at the study site were used to determine the level of tidepools. The height of the bench mark relative to zero tide level was obtained from surveying data. Depths, perimeters, widths, and lengths of the pools were measured. The study pools were categorized into 4 vertical zones along the shore as follows: upper (2.3 to 3.5 m from the zero tide level), middle (1.9 to 2.3 m), lower (0.6 to 1.9 m), and base (–0.3 to 0.6 m). These tidal elevations represent different degrees of emergence and submergence. The tide is mixed semi-diurnal with maximum high tides about 3.96 m and extreme low tides about 0 m (Dr N. J. Wilimovsky unpubl.).

Fish specimens were sampled from the tidepools during low tides (usually within an hour of low tide) with emulsified rotenone ichthyocides. Fish were measured (standard length) to the nearest 0.1 mm and weighed to the nearest 0.01 g directly after collection in a small field laboratory on the island. Sagittal otoliths were removed for ageing purposes. After these measurements the specimens were fixed in 10 % buffered formalin and later washed in freshwater and transferred to 37.5 % isopropanol before lodging the specimens in the University of British Columbia Ichthyology collection. Ageing data from otoliths were verified by using length-frequencies analyzed by a computer program designed to fit normal distributions to polymodal data (MacDonald & Pitcher 1979, MacDonald 1980). The basic assumption of this program is that the length-frequencies are mixtures of normal distributions.

Abundance estimates were made from censuses of collections of the 2 tidepool resident species. Density of Clinocottus globiceps and Oligocottus maculosus was calculated by dividing the number of individuals by the tidepool area (fish m^{-2}). Production estimates were made following the instantaneous growth rate method (Ricker 1946, Ricker & Foerster 1948). Mean annual production was estimated for each species for collections taken from July 1986 to July 1987 and from August 1987 to October 1988 (referred herein as first and second year respectively). Production estimates for the second year were corrected to annual values by multiplying by 365/404. Production was described on an area basis, as most aquatic production is known to depend on area (Le Cren 1972). Production estimates were calculated by tidal zones and ANOVA was used to determine if significant differences existed among zones. All statistical inferences were based on a significance level of $\alpha = 0.05$.

RESULTS

Distribution of Clinocottus globiceps and Oligocottus maculosus within the study area

Clinocottus globiceps and Oligocottus maculosus are both bottom-dwelling and often occur sympatrically, although C. globiceps tended to favour the mid to lower intertidal pools. C. globiceps was collected from pools as high as 2.70 m above zero tide level, but occurred in greatest numbers in middle and lower tidepools (Table 1, Fig. 1). O. maculosus, though widely distributed, was concentrated in the middle and higher level tidepools (Table 1, Fig. 2). O. maculosus could be found in fair abundance in the more rocky pools with only moderate amounts of macrophytic cover. It frequently occurred in great numbers in open sandy areas of some tidepools.

The vertical range inhabited by Clinocottus globiceps and Oligocottus maculosus reflected the size of the fish. Larger C. globiceps, although found throughout the area, were more concentrated on the lower level than were smaller fish. Young C. globiceps were usually found at tide levels between 0.70 and 1.50 m (Fig. 1). Juveniles less than 25 mm were not common in pools inhabited by adults. Young O. maculosus did not occur as low as did older fish. Larger O. maculosus were found inhabiting pools as high as those inhabited by juveniles (Fig. 2). However, the observed variation in the relative abundances at different zones (Figs. 1 & 2) was found to be statistically non-significant (Table 2). The lack of significance among zones is likely to be masked by the high variability within zones.

Density

Mean densities of both species varied considerably in all zones during the 2 yr period. There were no specimens collected from the upper and base zones during the first and second year respectively (Table 1). Densities of all ages in 1987–88 collections were usually less in the upper and middle levels than in the lower zone for Clinocottus globiceps, whereas Oligocottus maculosus had higher densities in the upper to middle zones than in the lower zone (Table 1, Fig. 3). Densities of O. maculosus were generally higher than

Table 1. *Clinocottus globiceps* and *Oligocottus maculosus*. Mean annual density (N; no. m^{-2}), mean annual biomass (B; g m^{-2}), mean instantaneous growth rates (G), annual production (P; g m^{-2} yr^{-1}) and production to biomass ratio (P:B). Production and biomass for 1987–88 are based on corrected annual values obtained by multiplying by 365/404. –: no data

| | July 1986 – July 1987 | | | | August 1987 – October 1988 | | | |
	Upper	Middle	Lower	Base	Upper	Middle	Lower	Base
Clinocottus globiceps								
N	–	2.7	1.9	1.2	0.7	1.0	7.5	0.6
B	–	21.1	11.3	8.3	1.8	2.6	26.0	–
G	–	0.51	0.78	0.57	0.94	0.77	0.66	–
P	–	10.8	8.8	4.7	1.7	2.0	17.2	–
P:B	–	0.51	0.78	0.57	0.94	0.77	0.66	–
Oligocottus maculosus								
N	–	2.2	5.3	0.1	15.6	15.7	9.8	–
B	–	1.8	4.9	0.04	9.3	13.1	7.6	–
G	–	1.00	0.76	0.80	1.20	1.04	1.09	–
P	–	1.8	3.7	0.03	11.2	13.6	8.3	–
P:B	–	1.00	0.76	0.80	1.20	1.04	1.09	–

those of *C. globiceps*. Relative differences among zones for both species were fairly constant among years, as indicated by the lack of significant zone × year interaction (Table 2). Similar trends were found for biomass of both species (Table 1).

The surface area of pools was significantly correlated with density of *Clinocottus globiceps* , but there was only a weak and non-significant negative correlation between density of *Oligocottus maculosus* and surface area of pools (Table 3). Depth of pools correlated negatively with density for *O. maculosus*; however there was no correlation between these 2 variables for *C. globiceps* (Table 3).
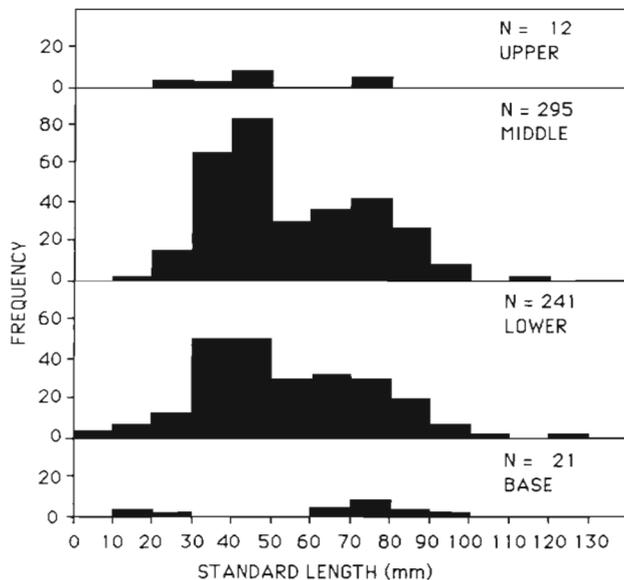
Growth

There were large yearly differences in growth within zones, but no significant differences were found among zones (Table 2). There was no significant relationship between population density and growth rate (Table 3); the amount of variability in
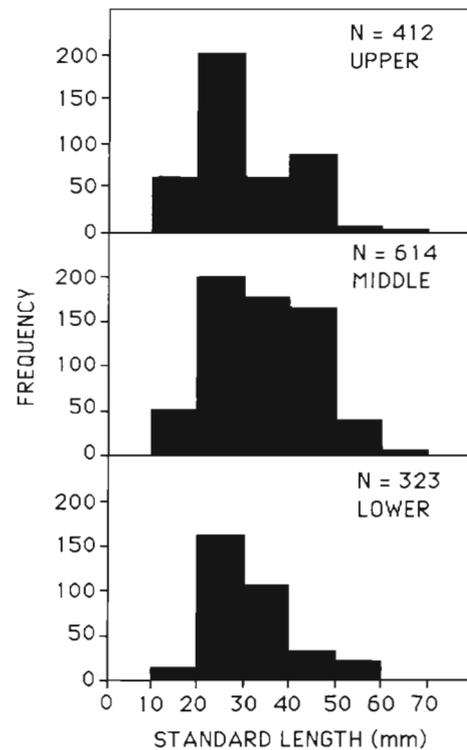

Fig. 1. *Clinocottus globiceps*. Length frequency distribution from tidepools at different levels

Fig 2. *Oligocottus maculosus*. Length frequency distribution from tidepools at different levels; there were no data for the base zone

Table 2. *Clinocottus globiceps* and *Oligocottus maculosus*. Analyses of variation in growth, density, biomass and production. Data classification by zone and by year (both fixed factors)

Source of variation		*Clinocottus globiceps*				*Oligocottus maculosus*		
	df	MS	F-ratio	p	df	MS	F-ratio	p
Growth								
Year	1	0.1070	0.94	0.35	1	0.1260	1.05	0.32
Zone	1	0.1709	1.50	0.24	1	0.0329	0.44	0.52
Zone × year	1	0.2326	2.04	0.17	1	0.0195	0.26	0.62
Error	16	0.1141			12	0.0743		
Total	19				15			
Density								
Year	1	0.4671	0.04	0.85	1	210.2645	1.79	0.21
Zone	1	28.7909	2.40	0.14	1	45.3809	0.39	0.55
Zone × year	1	35.1182	2.93	0.10	1	23.6696	0.20	0.66
Error	19	11.9762			11	10.6991		
Total	22				14			
Biomass								
Year	1	371.4819	1.20	0.29	1	145.6370	1.90	0.20
Zone	1	237.7747	0.77	0.39	1	33.1877	0.43	0.53
Zone × year	1	478.5106	1.54	0.23	1	32.4460	0.42	0.53
Error	19	310.0686			10	76.5071		
Total	22				13			
Production								
Year	1	122.7273	1.64	0.22	1	99.2201	1.74	0.22
Zone	1	82.4755	1.10	0.31	1	34.2435	0.60	0.46
Zone × year	1	75.8039	1.01	0.33	1	10.1877	0.18	0.68
Error	19	74.6931			10	57.1737		
Total	22				13			

growth explained by changes in density was very low ($r^2 = 0.001$ and 0.01 for *Clinocottus globiceps* and *Oligocottus maculosus* respectively) and statistically non-significant. Correlations of density and growth rates between age groups 2+ and 3+ for *C. globiceps* and 1+ and 2+ for *O. maculosus* were positive but

Table 3. *Oligocottus maculosus* and *Clinocottus globiceps*. Summary of correlation analyses. r^2 values are the proportion of the total variation accounted for by the independent variable. N: density; G: instantaneous growth rate; B: biomass; P: production. Subscripts 1, 2 and 3 refer to age groups 1+, 2+ and 3+ respectively

Variables		*Oligocottus maculosus*				*Clinocottus globiceps*		
	df	r	r^2	p	df	r	r^2	p
N with depth	10	−0.68	0.46	0.016	14	0.19	0.04	0.480
N with area	10	−0.25	0.06	0.442	14	0.56	0.31	0.024
G with B	11	−0.13	0.02	0.663	16	−0.06	0.004	0.809
G_1 with B_1	6	−0.35	0.13	0.391	6	−0.10	0.01	0.809
G_2 with B_2	11	0.24	0.06	0.438	11	0.02	0.001	0.936
G_3 with B_3	8	−0.03	0.001	0.945	7	−0.68	0.47	0.040
G with N	11	−0.10	0.01	0.734	16	−0.03	0.001	0.913
G_1 with N_1	6	−0.43	0.18	0.292	6	−0.32	0.10	0.440
G_2 with N_2	11	0.22	0.05	0.473	11	−0.15	0.02	0.620
G_3 with N_3	8	−0.04	0.002	0.906	7	0.73	0.53	0.030
G_1 with P_1	6	−0.01	0.0001	0.985	6	0.04	0.002	0.928
G_2 with P_2	11	0.42	0.18	0.154	11	0.32	0.10	0.292
G_3 with P_3	8	0.57	0.32	0.086	7	0.54	0.29	0.130
P with B	11	0.98	0.96	0.000	15	0.92	0.85	0.000
P with G	11	−0.14	0.02	0.645	16	0.06	0.004	0.815
P with depth	10	−0.45	0.20	0.139	14	0.23	0.05	0.383
P with area	10	−0.04	0.002	0.902	14	−0.25	0.06	0.357
P with perimeter	10	−0.10	0.02	0.690	14	−0.37	0.14	0.159

non-significant in the latter species (Table 3).

There was a significant correlation ($r = -0.68$, $p <$ 0.05) between growth and mean biomass for *Clinocottus globiceps* between age groups 2+ and 3+; the correlation for *Oligocottus maculosus* between age groups 1+ and 2+ was positive, but weak (Table 3).

Production

Annual production for the 2 species in all zones was 8.1 and 7.0 g m^{-2} yr^{-1} in the first and second year respectively for *Clinocottus globiceps*, and 1.8 and 11.0 g m^{-2} yr^{-1} over the same period for *Oligocottus maculosus*. About 33 % of *C. globiceps* production in the second year occurred between ages 1+ and 2+, whereas 65 % of *O. maculosus* production occurred between ages 1+ and 2+ during the same period. Production was small between ages 0+ and 1+ in both species because of the lower densities of these age groups.

Production in 1987–88 was greater in the lower zone than in the upper and middle zones for *Clinocottus glo-*
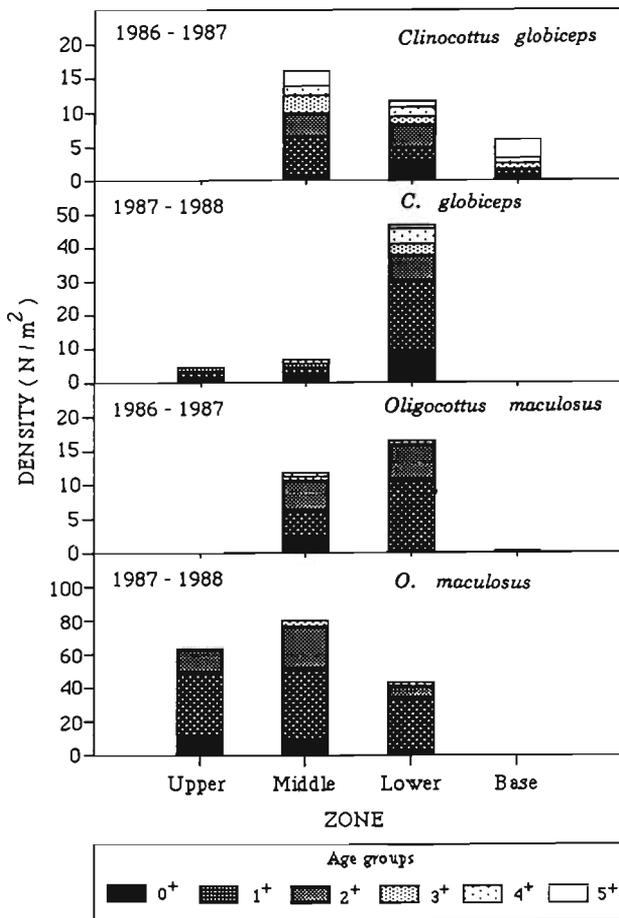

Fig. 4. *Clinocottus globiceps* and *Oligocottus maculosus*. Production by age group in each zone for the period 1986–87 to 1987–88
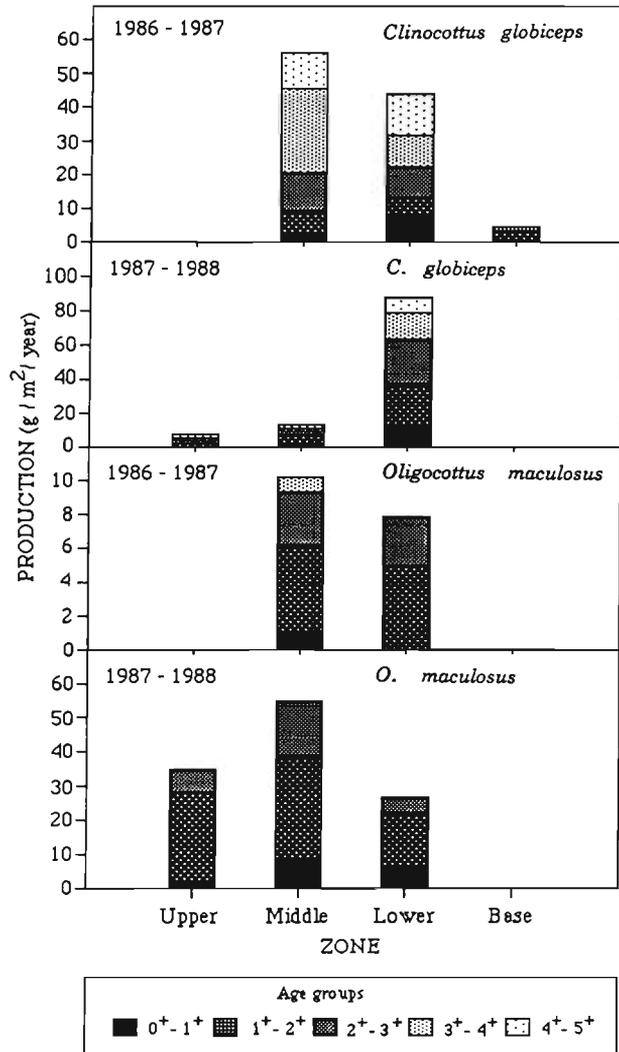

Fig. 3. *Clinocottus globiceps* and *Oligocottus maculosus*. Density by age group in each zone for the period 1986–87 to 1987–88

biceps, and in *Oligocottus maculosus* it was greater in the upper and middle zones than in the lower zone (Table 1, Fig. 4). Annual production estimates for *O. maculosus* in the upper and middle zones were 11.2 and 13.6 g m^{-2} yr^{-1} respectively, with corresponding values for *C. globiceps* being 1.7 and 2.0 g m^{-2} yr^{-1} respectively. Production estimates for *O. maculosus* and *C. globiceps* in the lower zone were 8.3 and 17.2 g m^{-2} yr^{-1} respectively. There was a lack of significant interaction of zone with year (Table 2).

Production was poorly correlated with instantaneous growth rates for most age groups (Table 3). For all age groups combined, variability in growth accounted for less than 0.4 and 2 % of changes in year class production for *Clinocottus globiceps* and *Oligocottus maculosus* respectively. Production was positively correlated

with mean biomass for both species and fluctuations in mean biomass accounted for 85 and 96 % of fluctuations in production rates of *C. globiceps* and *O. maculosus* respectively (Table 3).

Depth varied substantially among pools with values ranging from 0.1 to 1.9 m. There was a positive but non-significant correlation between tidepool depth and production ($r = 0.23$, $p > 0.05$) for *Clinocottus globiceps*. However, the correlation between depth and production for *Oligocottus maculosus* was negative ($r = -0.45$, $p > 0.05$). Surface area and perimeter were not significantly correlated with production (Table 3).

Production to biomass (P:B) ratios

Annual production to biomass ratios (P:B) were lower for the larger species (*Clinocottus globiceps*) and higher for the smaller species (*Oligocottus maculosus*) (Table 1). There were annual variations in P:B ratios, with 1986–87 having lower values than 1987–88. P:B ratios also varied among zones with the upper zone having the highest P:B ratios for both species, and middle and lower zones having the lowest ratios for *C. globiceps* and *O. maculosus* respectively (Table 1).

DISCUSSION

Distribution of tidepool cottids within the intertidal area can be influenced by many interacting factors. For example, a great amount of habitat cover, primarily large rocks and crevices, but also dense algal and seagrass growth, allowed *Clinocottus globiceps* to inhabit higher, often shallower pools, a habitat more suitable to *Oligocottus maculosus* (Nakamura 1976a). How long a pool is actually emerged or submerged may also affect the distribution of intertidal fishes (Green 1971b, Nakamura 1976b).

Numerical abundance estimates are very reliable, as all fish were collected from each habitat. However, it was not possible to differentiate between fluctuations in abundance attributable to mortality or emigration. Although tidepools are not entirely closed systems, the strong homing tendencies of these species (Green 1971b, 1973) make emigration seem far less likely in causing density fluctuations. Predation is considered to be the most general cause of natural mortality in fish populations (Beverton & Holt 1957). There is no direct evidence from the present study to suggest that *Clinocottus globiceps* and *Oligocottus maculosus* are eaten by other tidepool fishes. Predation has rarely been observed in intertidal fishes and probably does not constitute an important factor controlling the populations of intertidal fishes (Gibson 1982).

Production of *Oligocottus maculosus* (11.0 g m^{-2} yr^{-1}) was higher than *Clinocottus globiceps* (7.0 g m^{-2} yr^{-1}) in the second year (Fig. 4). Young age groups (1+ and 2+) made a significant contribution to production. For example, age groups 1+ and 2+ in *O. maculosus* contributed 65.4 % of total production. Young fish are the most productive and may contribute up to 95 % of the total production (Mann 1971, Mathews 1971, Chadwick 1976).

Moring (1976) reported average densities of 1.64, 2.66, and 2.86 fish m^{-2} of 'effective sampling area' for *Oligocottus maculosus* at 3 sites in Trinidad Bay, California. These densities are substantially lower than densities of 9.8 to 15.7 fish m^{-2} reported in the present study. This difference is consistent with the observation that densities of *O. maculosus* increase as one moves northward away from the southern limits of their range (Yoshiyama et al. 1986). Mean biomass for *O. maculosus* and *Clinocottus globiceps* was 11.4 and 10.5 g m^{-2} respectively. Annual variations in biomass and production of the 2 species were closely and positively linked to changes in population numbers in the tidepools at Helby Island. Annual variation in growth was little, and for the most part did not correlate with density (Table 3), indicating that densities did not generally regulate growth. Production of *C. globiceps* and *O. maculosus* was probably influenced by factors controlling density.

Population density of both species as expressed by age varied from year to year, but remained relatively stable within zones (Fig. 3). Carrying capacity may be determined by available habitat and foraging sites, with migration to and retention within pools having available suitable habitat (Chapman 1966, Bachman 1984). The amount of suitable habitat available may be size or age dependent, resulting in different size or age structure among zones (Bohlin 1978). The present study has shown that *Clinocottus globiceps* populations exhibit a tendency for larger individuals to inhabit lower rather than higher level pools (Fig. 1).

Production as examined by zones for the 2 species reflects the mean biomass of the 2 species. The ratio of production to biomass indicates the turnover rate of production of the habitat. Annual P:B ratios were generally not constant among zones. Since growth among zones was not significantly different, it is reasonable to assume that the P:B ratios were reflecting the size and age structure of the zones. However, it is worth noting that a lack of significant variations in growth among zones as indicated by ANOVA (Table 2) may have resulted from a lack of consistent differences among vertical location of pools rather than a lack of variability.

The production estimates obtained in this study indicate that tidepools may support substantial secondary production. However, these estimates should be

treated with caution for the following reasons. Firstly, the younger age groups (0+ and 1+) were not adequately represented in the samples. This discrepancy has been shown in other tidepool cottids (Grossman 1982, Yoshiyama et al. 1986) and is probably attributable to the passive dispersal of the planktonic larval phase of these species which in turn influences recruitment into tidepools. Secondly, the study pools were probably not optimal habitats for older fish. There were very few *Clinocottus globiceps* and *Oligocottus maculosus* older than age 4+, hence their contribution to production was not substantial. Perhaps large individuals, especially *C. globiceps*, are in pools where waters are more turbulent and deeper, and thus are difficult to sample.

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