A COMPARATIVE ANALYSIS OF THE ECOLOGY AND NICHE PARTITIONING IN TWO SPECIES OF THE FISH GENUS PHOLIS (PHOLIDIDAE)

by

GRANT WILLIAM HUGHES

B.Sc., University of Victoria, 1976

ACCEPTED
FACULTY OF GRADUATE STUDIES
[redacted]
Acting DEAN
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We accept this thesis as conforming to the required standard.

[redacted]
J.E. McInerney

[redacted]
P.T. Gregory

[redacted]
M.B. Hocking

[redacted]
A.E. Peden

UNIVERSITY OF VICTORIA
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Supervisor: Dr. J.E. McInerney

ABSTRACT

The ecological relationship between two syntopic pholidid fishes, *Pholis laeta* and *P. ornata* was investigated to determine what factors were involved in the reduction of niche overlap in Saanich Inlet, Vancouver Island, British Columbia. Niche breadths and life histories were also compared. Data were collected by monthly beach seining, intertidal trapping, stomach sample analysis, laboratory activity rhythm recording and laboratory breeding observations.

Both *P. laeta* and *P. ornata* occur in the eelgrass beds during the summer months and show niche separation which may facilitate coexistence. Microhabitat use of the eelgrass depths, intertidal habitat use, prey type, and characteristic location of prey taken differ between species in fish of one year and older. Young of the year of both species share similar habitat and food. Food sizes increase with fish size but were similar in both species. Activity patterns were similar in both species. *P. ornata* average greater diversity of resource use than *P. laeta* and has a wider niche.

Both species are absent from the eelgrass during the winter months. *P. laeta* breed in the rocky intertidal and shallow subtidal zone in the absence of *P. ornata* during this time period. Eggs are guarded by one or both parents and hatch in early spring.

Growth rates of both species are similar although *P. laeta* live longer than *P. ornata* and grow to a larger size. Mortality rates are lower in *P. laeta* which, when combined with increased fecundity due to larger maximum size, may result in the greater abundance of this species compared to *P. ornata*.

Examiners: [redacted]

J.E. McInerney

[redacted]

P.T. Gregory

[redacted]

M.B. Hocking

[redacted]

A.E. Peden

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Introduction

The gunnel family (Pisces: Pholididae) is one of the more specialized groups of northern blennies distributed throughout the North Pacific, North Atlantic and Arctic Oceans (Yatsu 1981). Six species in 3 genera occur in shallow waters of British Columbia and are characteristically small fishes having long slender compressed bodies (Hart 1973). In southern British Columbia *P. laeta*, the crescent gunnel and *P. ornata*, the saddleback gunnel, often occur syntopically in eelgrass beds although *P. laeta* is also known generally in the intertidal zone and *P. ornata* on muddy bottom habitats (Hart 1973). Both *P. laeta* and *P. ornata* have been taken at depths to approximately 40 m (Hart 1973, Fitch and Lavenberg 1975), but are usually found shallower. In British Columbia and northward *P. laeta* are more commonly captured than *P. ornata*.

Both sympatric species have extremely similar morphologies and differ mainly in pigmentation pattern (Miller and Lea 1972, Hart 1973, Fitch and Lavenberg 1975), the presence or absence of an interorbital pore (Peden and Wilson 1977), or by the number of dentary teeth in adults (Peden and Hughes 1982 ms). Because of similarities in other morphometric characters, their similar size and co-occurrence in eelgrass beds of southern British Columbia and northern Washington it is possible that the two species are adapted to similar niches.

The Gause principle (Gause 1934) states that species cannot coexist for long if they too similarly use the identical resources (Schoener 1974). If resources were previously limiting, it is likely that species will have faced competitive effects (Slobochikoff and Schulz 1980) which could result in limiting similarity of resource use (MacArthur and Levins 1967) and niche shift due to differential selection of those individuals which could successfully avoid maximum competition. Natural selection may therefore result in the divergence of body size or food size taken (Leviten 1978) or in behavioural differences such as the food type taken or habitat selected by each species.

This study was conducted to quantify niche overlap and niche breadth of *P. laeta* and *P. ornata* along the dimensions of habitat use, food type, food size and activity patterns which form axes of a 4-dimensional niche hyperspace (Hutchinson 1957). In addition, little is known about the life history of these species so investigations were conducted to document growth, mortality and reproduction in the shallow waters of Saanich Inlet, British Columbia.

Materials and Methods

Study Areas

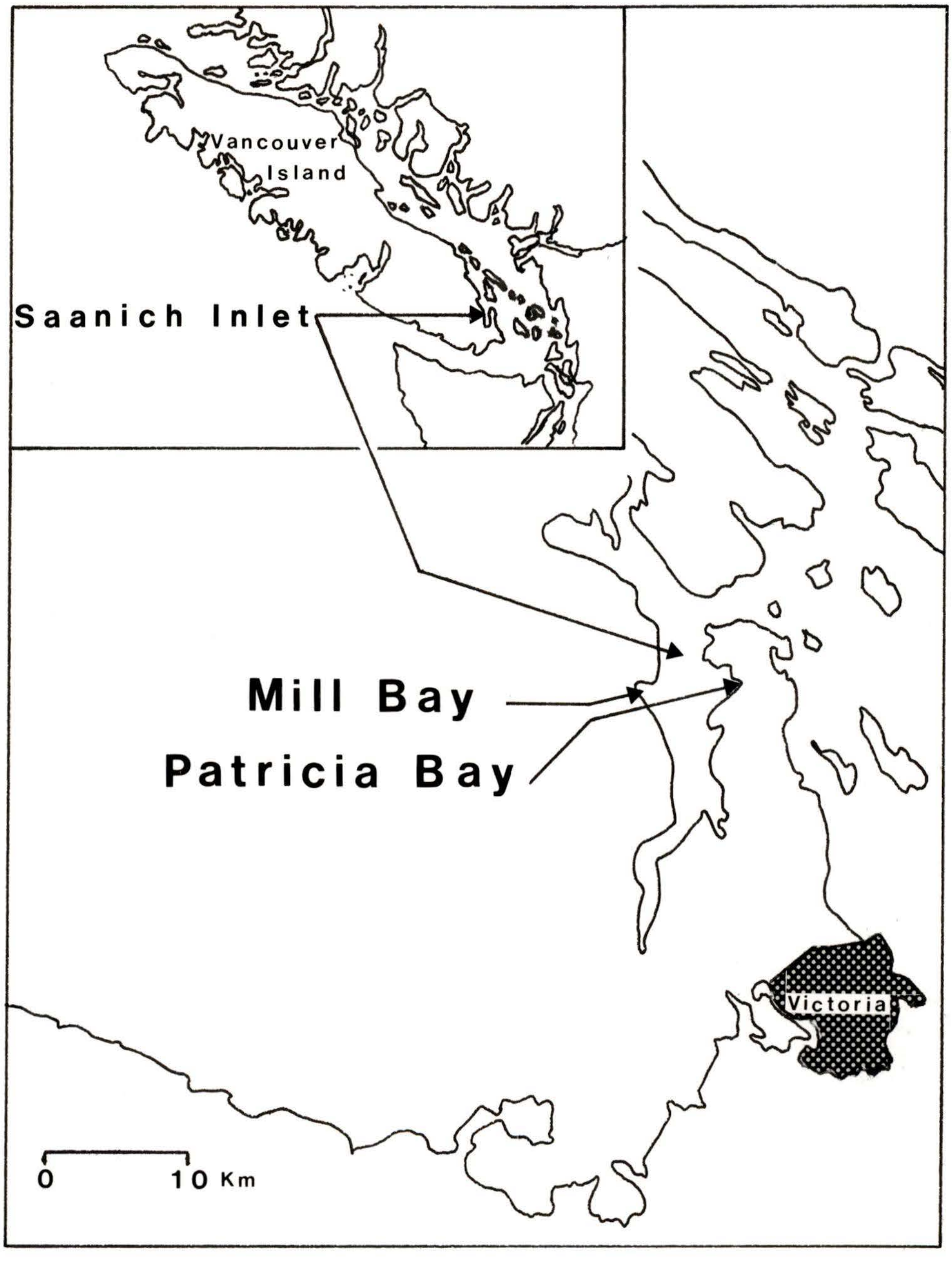
Two study areas in Saanich Inlet were selected (Figure 1) as both Patricia Bay and Mill Bay are characterized by lush subtidal eelgrass beds (*Zostera marina* L.), have presumed similar oceanographic conditions, and are easily accessible. The two localities differ somewhat in the slope of the beach (4.5% at Mill Bay versus 2.9% at Patricia Bay), and the presence of some small stones in the intertidal zone at Mill Bay compared with the nearly pure sand at Patricia Bay.

Determination of Habitat Utilization

Beach Seining

During the lowest tide series of each month in 1980 a census of *Pholis* at both study sites was made by beach seining along a permanent transect through the *Zostera* beds. Transects were constructed by staking two permanent markers in the beach ten meters apart at the water's edge when the tide was at a known height. The location of the transect was chosen after determining that eelgrass occurred subtidally offshore. The distance from the marker into the eelgrass bed to a depth of 0, 1 and 2 m below lower low water was measured at that time and recorded. Depths were determined using a plumb line lowered from a boat and distances from the markers to the depths selected were measured with a length of rope marked at one meter intervals. A 15 m long x 2 m deep beach seine net (10.0 millimeters (mm) stretch mesh) was deployed

Figure 1. Map showing study areas enlarged from a base map of British Columbia and Washington.


Vancouver
Island
Saanich Inlet
Mill Bay
Patricia Bay
Victoria
0
10 Km

from an inflatable boat and three hauls were made during each sampling series to remove fish from the succeeding depth zones of the eelgrass bed. (Rechecking of the stakes later using tide height predictions showed that the stake at Mill Bay was actually 0.25 m of depth higher up the beach than judged at the time that the transects were set out, although the Patricia Bay markers were more reliable. Therefore, the depths sampled differ by 0.25 m from the quoted 0, -1 and -2 at Mill Bay, although they are exactly repeatable from month to month). The areas seined are presented in Table 1. Areas above 0 m varied with the lowest tide height from month to month and were extrapolated from tide tables since tide height, time of day, slope of the beach, and the distance between the stakes were taken into account. Densities of gunnels in the different depth zones were calculated and tested to determine if there was an even distribution of each species throughout the depths using Kruskall Wallis analysis of variance by ranks (Zar 1974).

Water salinity and temperature were determined from 0, 1 and 2 m depth using a Yellow Springs Instrument Company temperature-conductivity salinometer.

Pholis collected from Mill Bay were anaesthetized in 0.075% propylene phenoxetol, enumerated and measured to the nearest millimeter standard length (SL). The dorsal or caudal fin of the anaesthetized fish was clipped to identify the depth zone from which a fish was collected. (This procedure was previously tested in the laboratory with no mortality of treated or untreated fish

TABLE 1

AREAS OF EELGRASS SEINED

Depth (m)	Mill Bay (m^2)	Patricia Bay (m^2)
Less than 0 m	variable	variable
0 to -1 m	175	390
-1 to -2 m	130	300

during a two month trial.) Fish were allowed to recover and were then returned to the midpoint of the zone of capture to avoid altering the population structure or density. The zone of subsequent recapture was recorded to determine if marked fish were recaptured in the zone from which they were originally captured using the Kolmogorov-Smirnov goodness of fit test (Zar 1974). This nonparametric test evaluates the null hypothesis that recaptured fish were evenly distributed in the 3 depth zones. As specimens were not uniquely marked it is possible that fish were recaptured more than once. Recaptures may therefore represent fewer specimens than recapture number would indicate but it has been assumed that this affects specimens from each depth stratum equally. The overlaps in the use of the eelgrass bed by the two species were computed using the symmetrical measure of Pianka (1973) using the depth zones as resources. Niche breadth calculations followed Levins (1968). In addition, the presence of other fish species were recorded for each sampling location (Appendix 1).

Pholis were seined from Patricia Bay and either kept alive for recording activity patterns, quick frozen on dry ice for otolith and stomach content analysis, or preserved in 10% neutralized formalin for stomach content analysis. Preserved fish were transferred to 40% isopropyl alcohol after one week in formalin. (Formalin preservation does not cause much regurgitation of stomach contents in Pholis, although regurgitation has been noted by Johnston (1954) for some Californian intertidal fishes.)

Vertical Distribution in Eelgrass

A fine (9.5 mm) mesh long handled net was used to sweep either the eelgrass canopy or the whole depth zone while wading in the eelgrass bed at low tide at Patricia Bay. Standard lengths of *Pholis* collected from the different strata were compared to see if a full range of fish sizes were caught in both strata.

Rocky Intertidal Captures

The rocky intertidal zone on the north side of the rocky breakwater approach to the dock at the Institute of Ocean Sciences, Patricia Bay, was examined for *Pholis* throughout 1980 by turning rocks. These specimens were removed during January and preserved to analyse maturity (egg size) and fecundity (egg number). Rocks from under which fish were removed were numbered by tying plastic markers with inscribed numbers, and examined at subsequent dates to index fish movement into the area. Additional rocks were also checked in subsequent months. *Pholis* captured in December were kept alive for analysis of breeding behaviour in the laboratory.

Rocky Subtidal Captures

During February and April 1980, two collections were made in the Patricia Bay area using SCUBA and fish toxicant (rotenone) at depths of 5 m and 12 m respectively. All *Pholis* were preserved and examined for state of maturity.

Intertidal Mudflat Captures

The relative abundances of *Pholis* that enter the intertidal zone at high tide were determined during the lowest tide sequences of early and mid-June 1981 at Patricia Bay. Two fine mesh traps (9.5 mm stretch mesh) with "V-shaped" leads 6.1 m length by 1.2 m height oriented away from the incoming tide were positioned in the low intertidal mudflat at low tide and then checked 24 hours later on the next low tide. The leads for the net were firmly staked to prevent fish from escaping underneath. Fish retreating from the intertidal zone were captured. The abundances of *Pholis* in the eelgrass zone at low tide were determined by beach seining at the end of the first week of trapping. The numbers of the two species collected by seining or trapping were tested to see if they represented the same ratio of P. *laeta* to P. *ornata* from the two microhabitats (Chi square contingency table with Yates correction, Zar 1974).

Food Utilization

Pholis were grouped by species into size groups of 20 mm and stomach contents were identified under a dissecting microscope with the aid of keys by Fulton (1968), Kozloff (1974), McLaughlin (1980), Smith and Carlton (1975) and Smith (1977). Each prey item was counted and the products of the two largest dimensions were recorded as an index of prey volume - termed effective area (EA) (Yoshiyama 1980) - as the prey were generally too small for determining volumetric displacement. EA corresponds to the dorsal area of an isopod or the lateral aspect of an amphipod for example, and does not include appendages in the measurement. The total amount of food in each stomach was calculated as the sum of the EA for each particular fish.

Concordance of the ranks of importance of the prey EA in each fish in each size grouping was determined using Kendall's W (Siegel 1956). Indexes of relative importance (IRI) (Pinkas *et al.* 1971) were calculated for each prey type as:

$$\begin{array}{l}\text{\% freq. of occurrence of}\\ \text{the prey taxon in any}\\ \text{amount, in fish of a}\\ \text{particular size class}\end{array} \; \mathrm{X} \left(\begin{array}{l}\text{\%age of diet}\\ \text{composed of}\\ \text{that prey tax-}\\ \text{on by number}\end{array} \; + \; \begin{array}{l}\text{\%age of diet}\\ \text{comp. of that}\\ \text{prey taxon by}\\ \text{effective area}\end{array}\right)$$

Kendall correlations between the diets of the size groupings were analyzed using the statistical algorithm provided by the Statistical Package for the Social Sciences (SPSS)(Nie *et al.* 1975). Diet diversity based on the number of prey items of different categories was calculated using Brillouin's formula (Poole 1974) using tabulation of $\log_{10} N!$ (Zar 1974). This measure is generally sample size dependent (Yoshiyama 1980) so the total numbers were standardized as percentages. This measure then relates to the diversity of feeding behaviour assuming prey items are taken individually.

Diets of each species were standardized using an estimation of number of young of the year based on logarithimic mortality of age groups (described in the section on young of the year). The adjusted proportion of food taken by an age class was computed by multiplying the proportion of the total number of fish in an age group (as discerned by analyses described in the section on aging) by the mean amount of food contained in the stomach of fish in each age group (see Roughgarden 1974). The total use of a food type in an age class (as a percentage of the total food usage) for each species was therefore estimated. The data were then cast into a two way table of age by food type, similar to Yoshiyama (1980). Calculation of total diet diversity (H_T), the weighted mean diversity of food types [$\Sigma u_i h_i(b)$], and the weighted mean diversity of size groups [$\Sigma v_j h_j(a)$] followed Pielou (1972). The values for $\Sigma u_i h_i(b)$ are the sum of μ_i (the proportion of the total occurrences that were of the ith fish age group) times $h_i(b)$ which is the food diversity of the ith size group. Values for v_j are the proportion of the total occurrences that were in the jth food type and $h_j(a)$ is the diversity of the fish size groups within that food type. Therefore, $\Sigma u_i h_i(b)$ is a measure of diet niche width of the species and $\Sigma v_j h_j(a)$ is a measure of the diet overlap of the species size groups.

Two factor analysis of variance analysed prey size for differences between species and size classes using SPSS. Logarithmic transformation eliminated heteroscedacity except in the smallest *P. laeta*, and then Mann Whitney U-tests (Zar 1974) were used to compare the size of prey taken in these 3 smallest size classes. Overlaps in food size were quantified using the method of

Pianka (1974). Niche breadth based on food size followed Levins (1968) with food size grouped to the nearest mm^2 and fish lengths grouped to correlate with age.

For both species, resource utilization spectra, niche width, mean niche location, within phenotype component (WPC) and between phenotype component (BPC) were analysed (Roughgarden 1974) using food size data and the adjusted proportion of food taken, described above. Fish were assigned to age groups based upon their length and each age grouping was considered to be a "phenotype" for this analysis.

Niche overlap measures (Pianka 1974) and niche breadth (Levins 1968) were calculated for the proportion of food taken by each combination of size class. As the reliability of overlap measures are subject to variation with species, collection date and location (Wallace and Ramsey 1983), only *Pholis* collected at Patricia Bay during the month of July were used except in the case of the certain size groups of specimens which were only present other months and so they were used for diet analysis of that size group. Principal components of the IRI of values of the diets were determined using the VARIMAX rotation option of SPSS.

In all cases the rarest food types accounting for a total of 5% or less of the total EA in each size group were excluded from analyses. The contribution of unidentified material was only considered in the food type overlap calculations. These calculations therefore result in maximal estimated overlap between the species size groups (perhaps artificially) - a procedure which may introduce a bias against the hypothesis that overlap is low along the food type niche dimension.

Activity Patterns

Laboratory Testing

Activity patterns over a 24 hour period, as indicated by fish movement in an enclosure suspended in an aquariumm, were recorded on a Cole Palmer Company Model 292-4 four channel event recorder. Two fish of each species were recorded simultaneously for a total of 44 fish, with each fish in an isolated 270 litre aquarium. Recording chambers consisted of a fibreglass enclosure (160 mm long by 70 mm wide by 50 mm high, mesh size 1.5 mm) suspended in an aquarium and attached to a single-pole single-throw switch which triggered the event recorder. Water flow and temperature (set to the mean temperature of the habitat at time of capture) were identical in each unit and the area was isolated from external disturbances.

Constant dark conditions were obtained by blocking out all windows and keeping all lights off. Natural photoperiod was obtained by allowing natural dawn and dusk conditions to be perceived through windows, with supplementary "daylight" fluorescent lighting from 6 a.m. until 9 p.m. This gave approximately 30 minutes of dawn and dusk, and normal (July 1981) daylengths.

Fish were collected from Patricia Bay at low tide during July of 1981, allowed to adjust for 1 hour in the chamber from which recordings were made, and then recorded for 24 hours. The mean percentage of recorded movements over a 1 hour span were then ranked for each species and correlations between the species were evaluated. Goodness of fit of activity throughout time to an even distribution was tested using Kolmogorov-Smirnov goodness of fit test (Zar 1974). Niche overlap (Pianka 1974) and breadth (Levins 1968) were calculated with data grouped into two hour intervals.

Field Testing

To determine if variation in the amount of food in the stomach of Pholis may be related to the time of day and not exclusively tide height, fish were captured on a similar low tide during the day and at night. Food in the stomach of fish of both species was quantified from collections made at 0530 PDT (dark) September 21, 1981 and 1030 PDT September 12, 1981 when the tide was low at 2.7' (0.8 m) at Mill Bay.

Life History

Aging and Growth

The ages of Pholis were determined from otoliths examined under a compound microscope and the lengths at the time of annulus formation were calculated by the method of Everhart et al (1975). The mean length of a cohort during a particular month was determined after subdividing length frequency histograms at the nodes where the greatest division between age classes was assumed to occur. The mean lengths and confidence limits of each cohort during May through October 1980 were used to document growth.

Estimation of Number of Young of Year

An estimate of the number of young of the year was determined by logarithmic regression of the number of fish of one year old, or older, with age. This was necessary as young of the year of both species are small enough to escape through the beach seine netting. Extrapolation from the mean number of one year olds to age = 0 using the calculated slope of the function enabled estimation of the number of young (Ricker 1975).

Breeding Behaviour

Maturing pairs of *P. laeta* were collected from Patricia Bay on December 9, 1980 and placed in closed (0.3 m x 0.3 m x 0.5 m length) aquaria with undergravel dolomite filtration and water temperature of 6°C. Cover was provided by transparent 5 mm thick acrylic sheets supported 20 mm or so above the dolomite. This was intended to simulate smooth stones under which the fish were found, but still enable viewing of the fish from above. Tanks were kept completely covered with black plastic to simulate the darkness of the 'underneath rock' habitat from which they were collected, and to minimize disturbances only a minimal amount of light was allowed in when observations of breeding behaviour were made. Qualitative observations were made daily at 0730, 1230 and 1730. Fish were not fed during 4 months of study and survived without apparent ill effects. I assumed that little feeding would occur in the wild at this time and sought to duplicate the condition in the laboratory.

In addition, maturing Pholis were captured from the Patricia Bay rocky intertidal area and examined for maturity and fecundity throughout winter months of 1979-80 and 1980-81.

Results

Habitat Distribution

Summer Eelgrass

Densities of *P. laeta* and *P. ornata* were highest during the summer months with both species being effectively absent during the winter (Figure 2). The dense *Zostera* during the summer and fall resulted in the beach seine rolling during one haul at Mill Bay (September -1 to -2 m) and many of the hauls at Patricia Bay. Density results are not overly affected by this as the subtidal microhabitat use was only being tested at Mill Bay where all the fish were returned to the area each time. Fish removed from Patricia Bay for other experiments however, were usually taken from closer to shore than the maximum distance to reach -2 m depths to avoid net rolling. *P. laeta* densities were consistently higher than *P. ornata* in the summer months. The retreat from the *Zostera* in November 1980 coincided with a marked decrease in surface water temperature and salinity (Figure 3, Appendix 2) and preceded, by at least two months, a lack of cover due to some dying off of the eelgrass. *P. laeta* were not significantly predisposed to occur in one of the three depth zones from June through September ($p > 0.10$) but *P. ornata* had its largest proportion in the shallowest depth zone ($p < 0.001$)(Figure 4) resulting in a smaller low tide habitat niche breadth (Table 2) for *P. ornata*. The average overlap of the proportions of each species in the eelgrass zones was 0.89 (Table 3). Fish captured and returned to one depth zone of the eelgrass

Figure 2. Densities of *Pholis laeta* (solid circles) and *P. ornata* (open circles) in the eelgrass bed at Mill Bay showing summer peak.

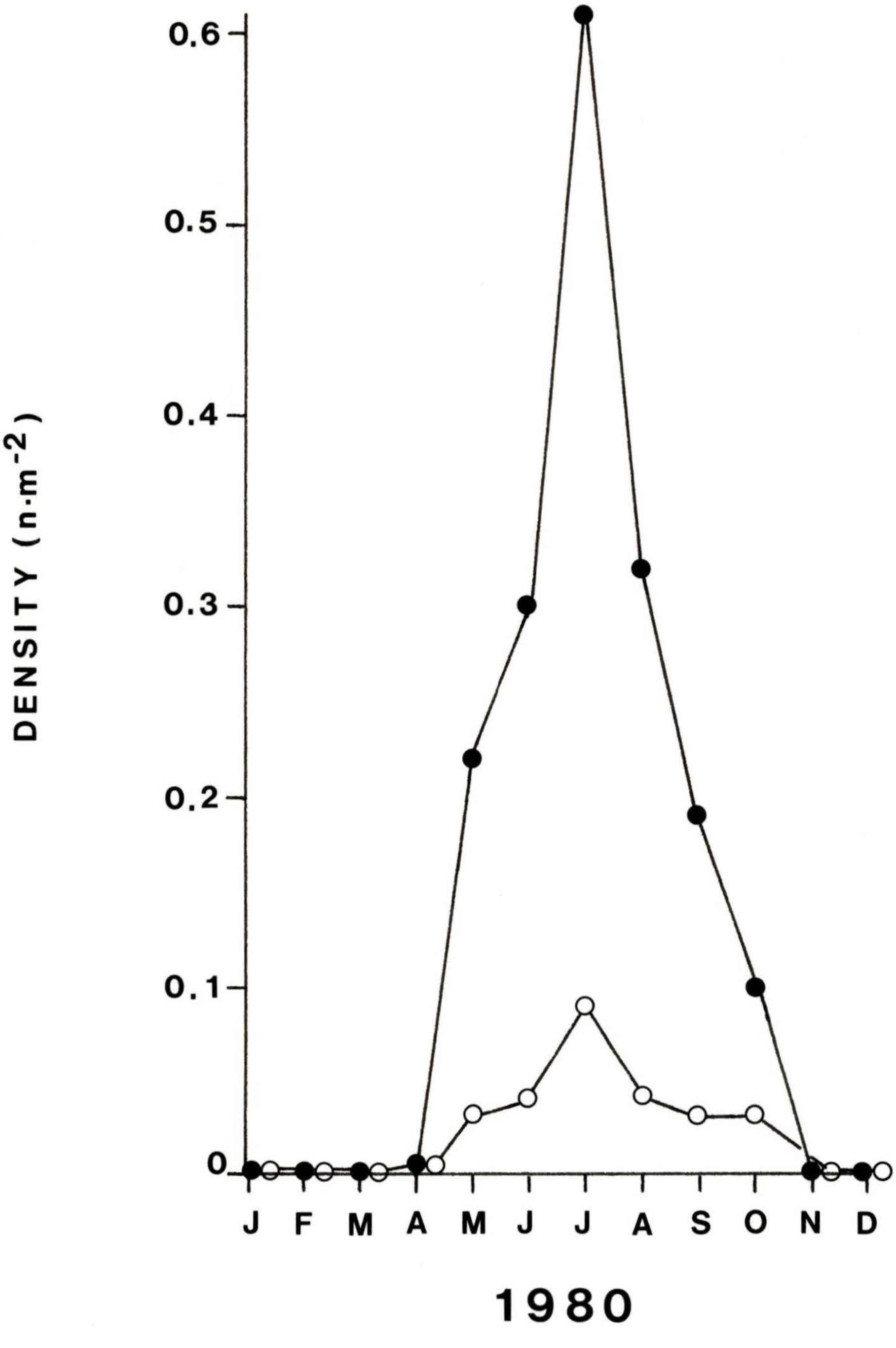

DENSITY (n·m-2)
0.6
0.5
0.4
0.3
0.2
0.1
0
J
F
M
A
M
J
J
A
S
O
N
D
1980

Figure 3. Monthly surface temperature and salinity at Mill Bay showing marked salinity change from October to November.

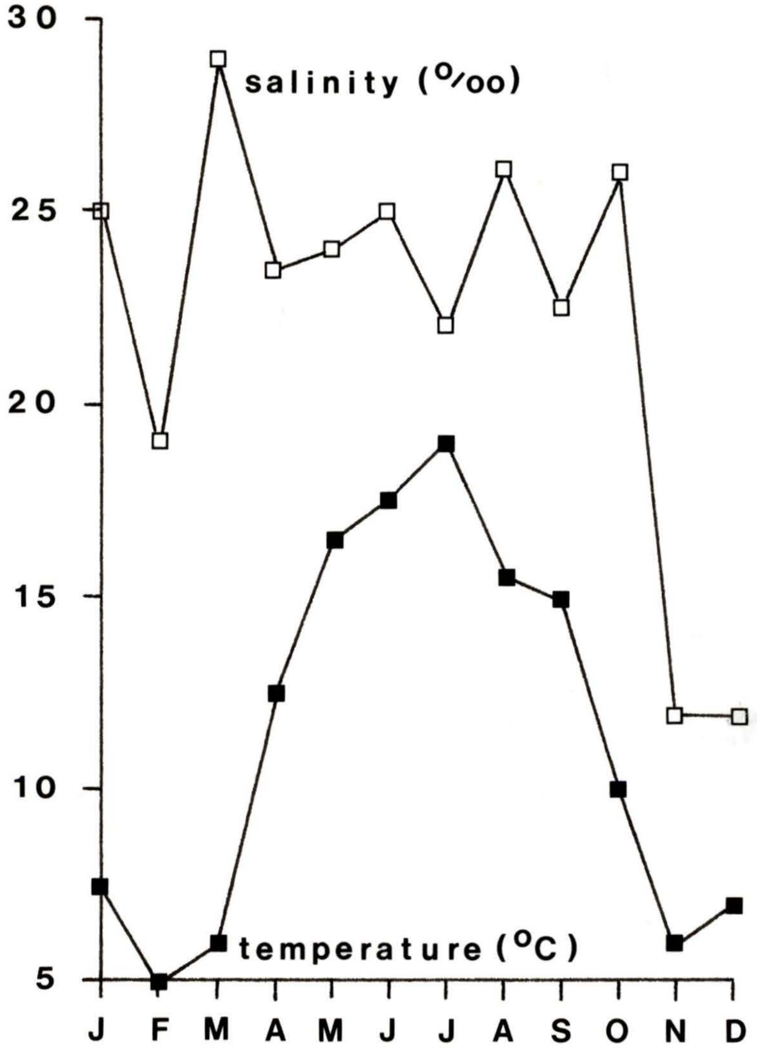

30
25
20
15
10
5
salinity (‰)
temperature (°C)
J
F
M
A
M
J
J
A
S
O
N
D

Figure 4. The distribution of *P. laeta* and *P. ornata* in the eelgrass bed at Mill Bay showing that *P. ornata* is likely to have maximum density in the shallowest depths at low tide. Rectangles are proportional in area to the amount of utilization of the depth zones by each species during each month. Total area equals 100% of sample for each species each month. Sample sizes shown below histograms.

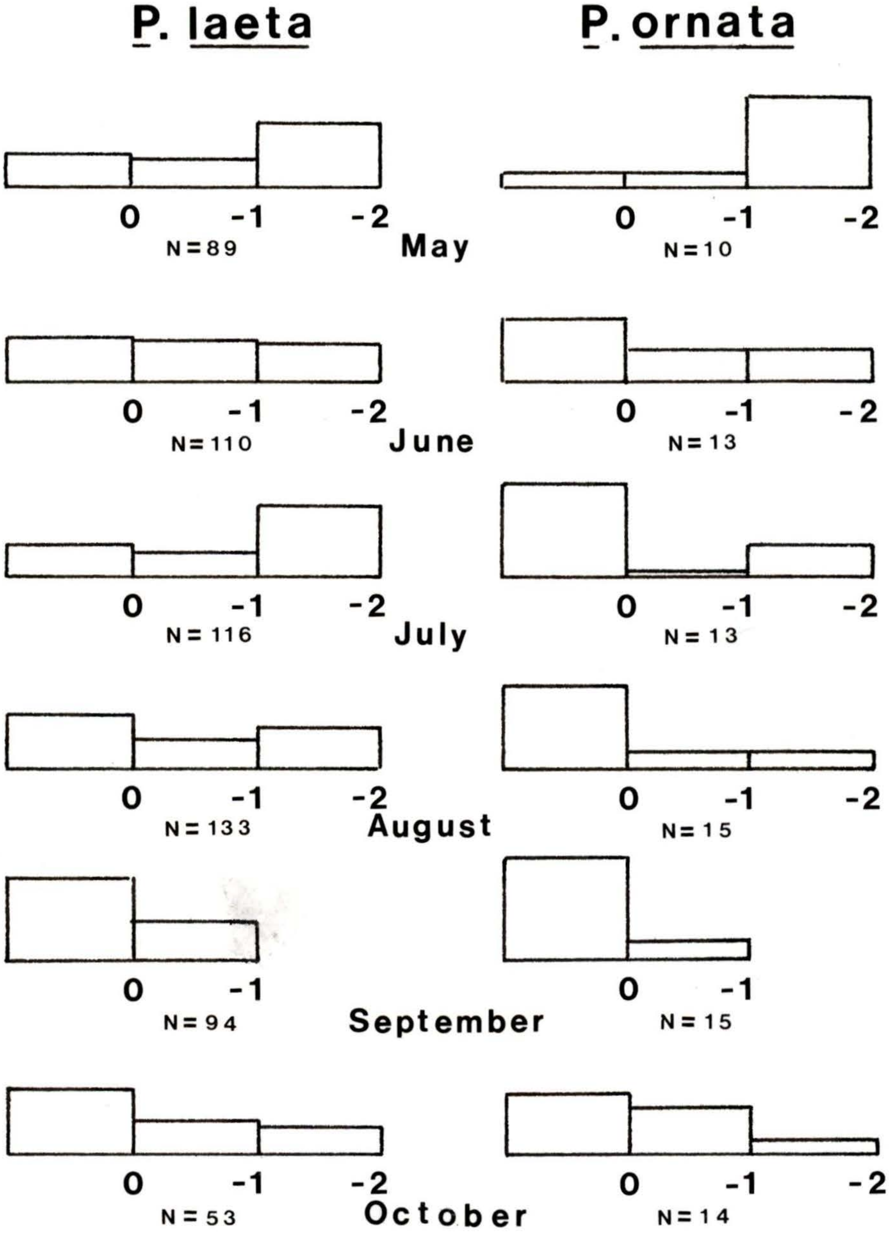

P. laeta
P. ornata
0
-1
-2
N=89
May
0
-1
-2
N=10
0
-1
-2
N=110
June
0
-1
-2
N=13
0
-1
-2
N=116
July
0
-1
-2
N=13
0
-1
-2
N=133
August
0
-1
-2
N=15
0
-1
N=94
September
0
-1
N=15
0
-1
-2
N=53
October
0
-1
-2
N=14

TABLE 2

WIDTH OF THE COMPONENTS OF THE NICHES OF *P. LAETA* AND *P. ORNATA* CALCULATED AS $(\Sigma Pi^2)^{-1}$

Dimension	*P. laeta*	*P. ornata*
Habitat - May 1980	2.63	1.68
- June 1980	2.99	2.67
- July 1980	2.35	1.70
- August 1980	2.83	1.97
- September* 1980	1.89	1.39
- October 1980	2.56	2.43
MEAN	2.67	2.09
Food type - fish size - 20-40 mm	1.05	2.82
- 40-60 mm	2.86	1.49
- 60-80 mm	2.44	2.66
- 80-100 mm	4.78	4.50
- 100-120 mm	3.71	5.66
- 120-140 mm	1.57	2.07
- 140-180 mm	2.63	-
MEAN	2.72	3.20

* no collection from deepest zone - not considered in averaging

(Table 2 continued .../)

TABLE 2 (continued)

WIDTH OF THE COMPONENTS OF THE NICHES OF *P. LAETA* AND *P. ORNATA* CALCULATED AS $(\Sigma Pi^2)^{-1}$

Dimension	*P. laeta*	*P. ornata*
Food size - fish age - 0 years	1.20	1.53
- 1 year	3.83	4.48
- older than 1 year	5.27	6.21
MEAN	3.43	4.07
Activity - Constant dark	5.76	8.34
- Photoperiod	6.75	6.22
MEAN	6.25	7.28

TABLE 3.

OVERLAP IN THE PROPORTIONS OF P. LAETA AND P. ORNATA IN EELGRASS

Month	Overlap*
May	0.94
June	0.96
July	0.63
August	0.91
September	0.94
October	0.97
Mean	0.89

* Overlap values can range from 0 (no similarity in use of eelgrass depth zones) to 1 (complete similarity in use of eelgrass depth zones).

were not likely to remain in that zone but were evenly distributed throughout the zones in subsequent captures after one month or longer (Table 4). Young of the year of both species were captured from the *Zostera* canopy but adults usually were not (Figure 5).

Summer Intertidal

Compared with the relative abundances of *P. laeta* and *P. ornata* in the eelgrass, significantly more *P. ornata* were captured in the intertidal traps (Table 5). In fact, although *P. laeta* was approximately 3 times as abundant as *P. ornata* in the eelgrass, at least twice as many *P. ornata* were captured in each intertidal sampling series (Figure 6). The overlap of the proportions of the two species between eelgrass and mudflat was 0.64.

Winter Captures

Breeding pairs and juvenile *P. laeta* occur under rocks in the intertidal zone during the winter but not during the summer, and evidently some movement between rocks occurs as fish replaced those removed in mid-January 1980 (Table 6). *P. ornata* were rarely found (only 1 specimen) in the intertidal zone at Patricia Bay. Many *P. laeta* and a few *P. ornata* were captured subtidally during early 1980 (Table 7) but none of the *P. ornata* were females.

TABLE 4

DEPTH OF RECAPTURED *PHOLIS* MARKED DURING SUMMER OF 1980

	P. laeta			*P. ornata*		
	Depth zone of marking			Depth zone of marking		
	>0	0 to -1 m	-1 to -2 m	>0	0 to -1 m	-1 to -2 m
Total marked	143	157	187	25	10	5
Number recaptured >0	6	4	5	2	0	0
Number recaptured 0 to -1	4	6	4	0	0	0
Number recaptured -1 to -2	0	2	3	0	0	0
Kolmogorov-Smirnov D	0.33	0.17	0.08	0.6	0	0
Probability of evenness	0.1<P<0.2	P>0.50	P>0.50	P>0.50	no data	no data

Figure 5. Size frequencies of *Pholis* captured in the eelgrass canopy (N = 15) and throughout the whole depth range (N = 61) illustrating that few large *Pholis* were caught from the canopy. Coding is *P. laeta* (shaded rectangles) and *P. ornata* (open rectangles).

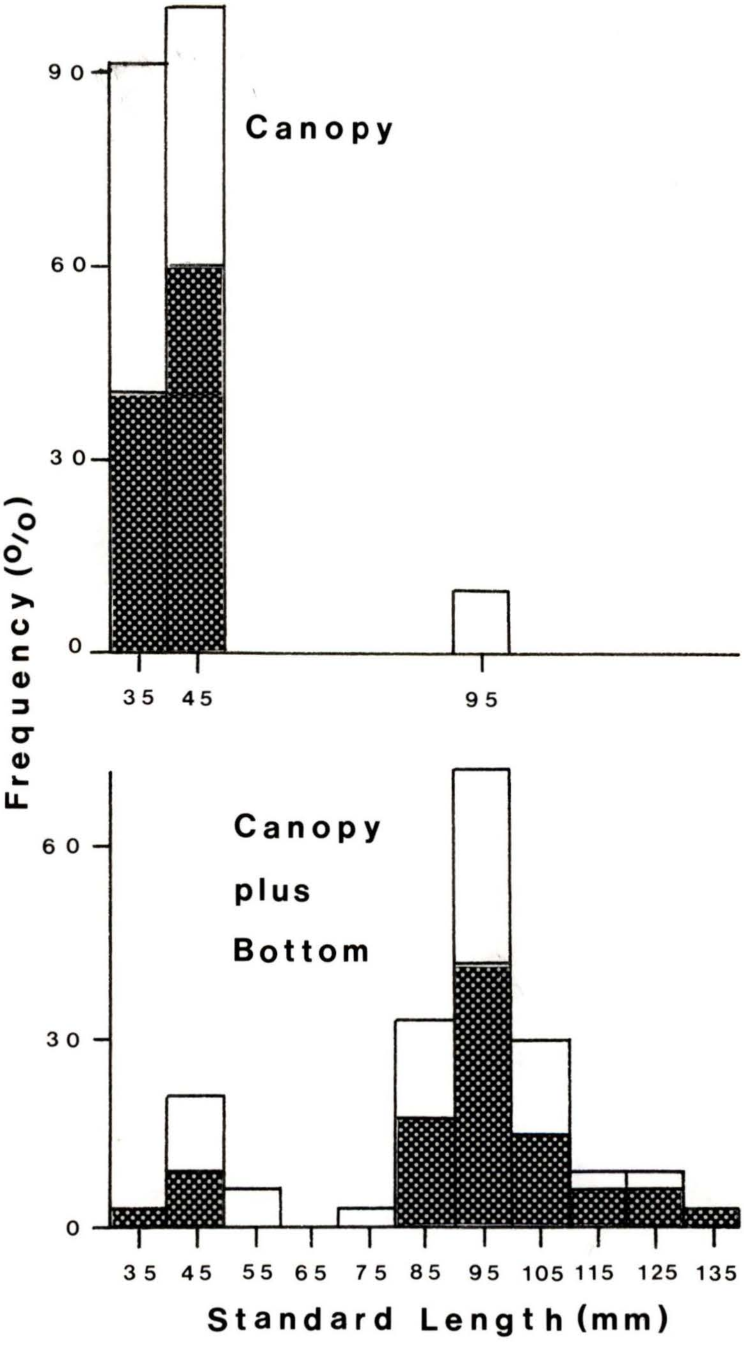

Canopy
90
60
30
0
35
45
95
Frequency (%)
Canopy
plus
Bottom
60
30
0
35
45
55
65
75
85
95
105
115
125
135
Standard Length (mm)

TABLE 5

CHI SQUARE CONTINGENCY TABLE OF GOODNESS OF FIT OF PHOLIS NUMBERS COLLECTED BY INTERTIDAL TRAPS TO NUMBERS IN EELGRASS BEDS

H_o: the relative numbers of the two species are independent of habitat

H_A: the relative numbers of the two species are not independent of habitat

First Trapping Series

	P. laeta	*P. ornata*	Total
Seining	174	60	234
Trapping	16	32	48
Total	190	92	

$\chi^2 = 28.66$

dF = 1

$p < 0.001$

Second Trapping Series

	P. laeta	*P. ornata*	Total
Seining	174	60	234
Trapping	12	38	50
Total	186	98	

$\chi^2 = 44.02$

dF = 1

$p < 0.001$

Figure 6. A comparison of the relative number of _Pholis_ captured in the subtidal eelgrass with the intertidal mudflat showing that a disproportionate number of _P. ornata_ enter the intertidal zone. a, intertidal traps (N = 96); b, eelgrass at Patricia Bay during period of trapping (N = 234); c, Mill Bay > 0m (N = 234); d, Mill Bay 0 to -1 m (N = 209); e, Mill Bay -1 to -2 m (N = 211).

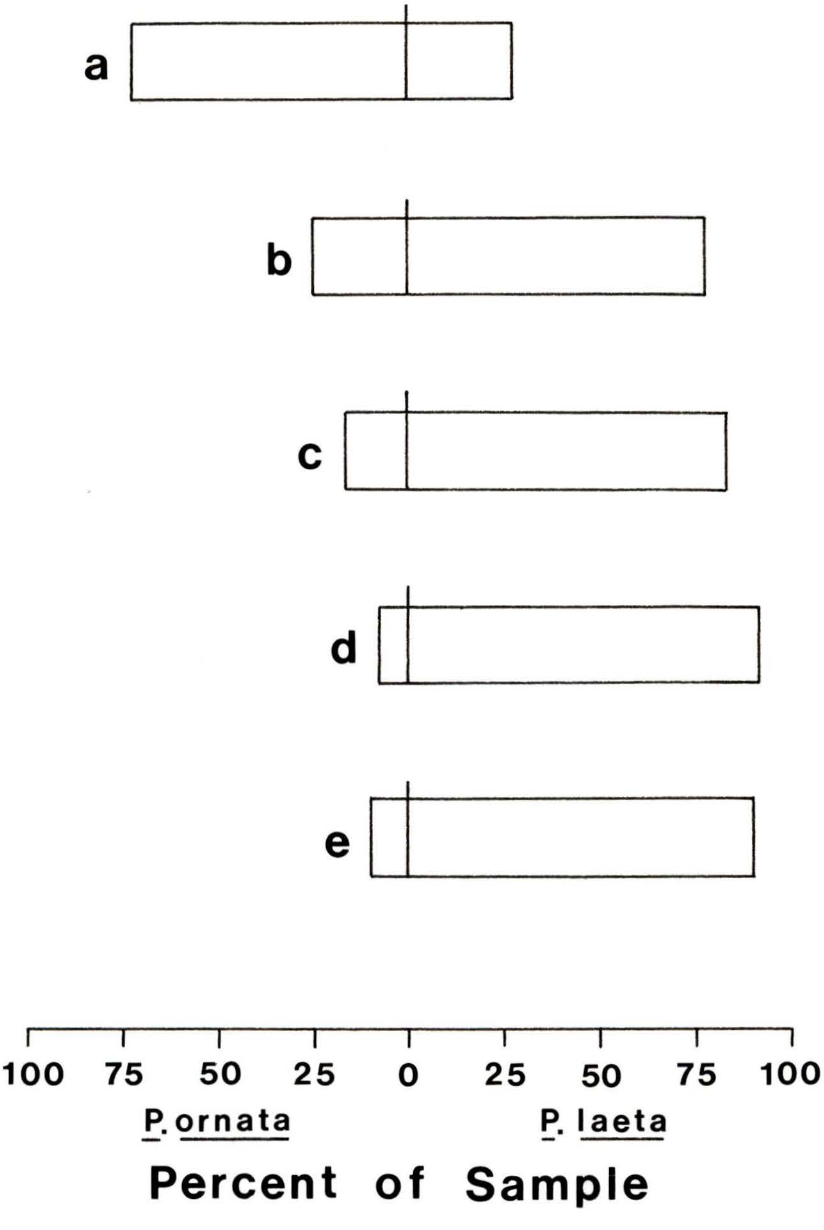

a
b
c
d
e
100
75
50
25
0
25
50
75
100
P. ornata
P. laeta
Percent of Sample

TABLE 6

FISH SPECIES HAND CAPTURED FROM UNDER ROCKS INTERTIDALLY AT PATRICIA BAY

Date	Number of Fish					Number of rocks checked
	P. laeta	*P. ornata*	*Anoplarchus purpurescens*	*Porichthys*	*Cottidae*	
January 17, 1980	32*	0	—	—	—	13
January 29, 1980	8**	0	many	0	some	11
February 14, 1980	24	0	24	0	0	17
April 18, 1980	7	0	some	1	few	7
May 7, 1980	4	0	25	4	0	18
June 14, 1980***	0	0	9	4	0	20
July 29, 1980***	0	0	0	0	0	21
November 22, 1980	10	0	1	0	1	—
December 9, 1980	14*	0	—	—	—	—
May 7, 1981	12+*	0	some	—	2	—
January 9, 1982	20*	1	prevalent	—	1	20

* removed
** only marked rocks checked
*** *Hemigrapsus* prevalent

TABLE 7

SUBTIDAL *PHOLIS* CAPTURES BY SCUBA WHEN *PHOLIS* NOT IN EELGRASS

Date	Depth (m)	*P. laeta* number	Notes	*P. ornata* number	Notes
February 29, 1980	5	41	spawned adults and juveniles	2	1 immature male 1 male (spent?)
April 15, 1980*	8-12	1	spent? male	2	males (spent?)

* 4 *P. clemensi* also captured

Food Utilization

Food Type

P. laeta (Figure 7) and P. ornata (Figure 8) show shifts in food type taken with growth. Both species feed mainly on harpacticoid copepods when small. P. laeta switch to a predominance of Caprella laeviscula, and P. ornata switch to a larger proportion of Macoma siphons and the tanaid (Leptochelius dubia) except at the largest size when the gammarid amphipod Anisogammarus pugettensis predominated. There is a marked separation in the use of caprellids and siphons by the two species (Figure 9). Diet concordance between individual fish was evident in more P. laeta size groups than in P. ornata (Table 8). Correlations of IRI rankings (Table 9) show decreases in dietary similarity between species, and within species when size differences are large (Figure 10). Diet diversity based on the number of prey of each type generally increased with size in both species (Figure 11).

The total diversity of the standardized matrix of food utilization was higher for P. ornata than P. laeta (Tables 10, 11). Niche breadth ($\Sigma u_i h_i$) was higher in P. ornata than P. laeta, and there was a lower overlap in food utilization between size classes of P. ornata than P. laeta ($\Sigma v_j h_j$).

Overlaps in food types taken are generally high in fish of similar size within species (Table 12) but decrease with increasing size difference both within and between species (Figures 12, 13). Diet niche breadth was largest in intermediate sized fish of both species (Table 2).

Figure 7. Indexes of relative importance of the prey items in the diet of _P. laeta_ of different size classes showing dietary shift with growth. Horizontal scale: percent frequency of occurrence of the prey in fish of a particular size class. Vertical scale above horizontal scale: the percentage of the total of all food taken by a size class based on prey surface area. Vertical scale below horizontal line: the percentage of the diet based on number of prey. Abbreviations used: Harpac = harpacticoida, Polych = polychaeta, Gammar = gammaridea, Tanaid = tanaidae, Caprel = caprellidae, Hippol = hippolytidae, Zost = _Zostera_, Brachy = brachiura. Sample sizes as in Table 8.

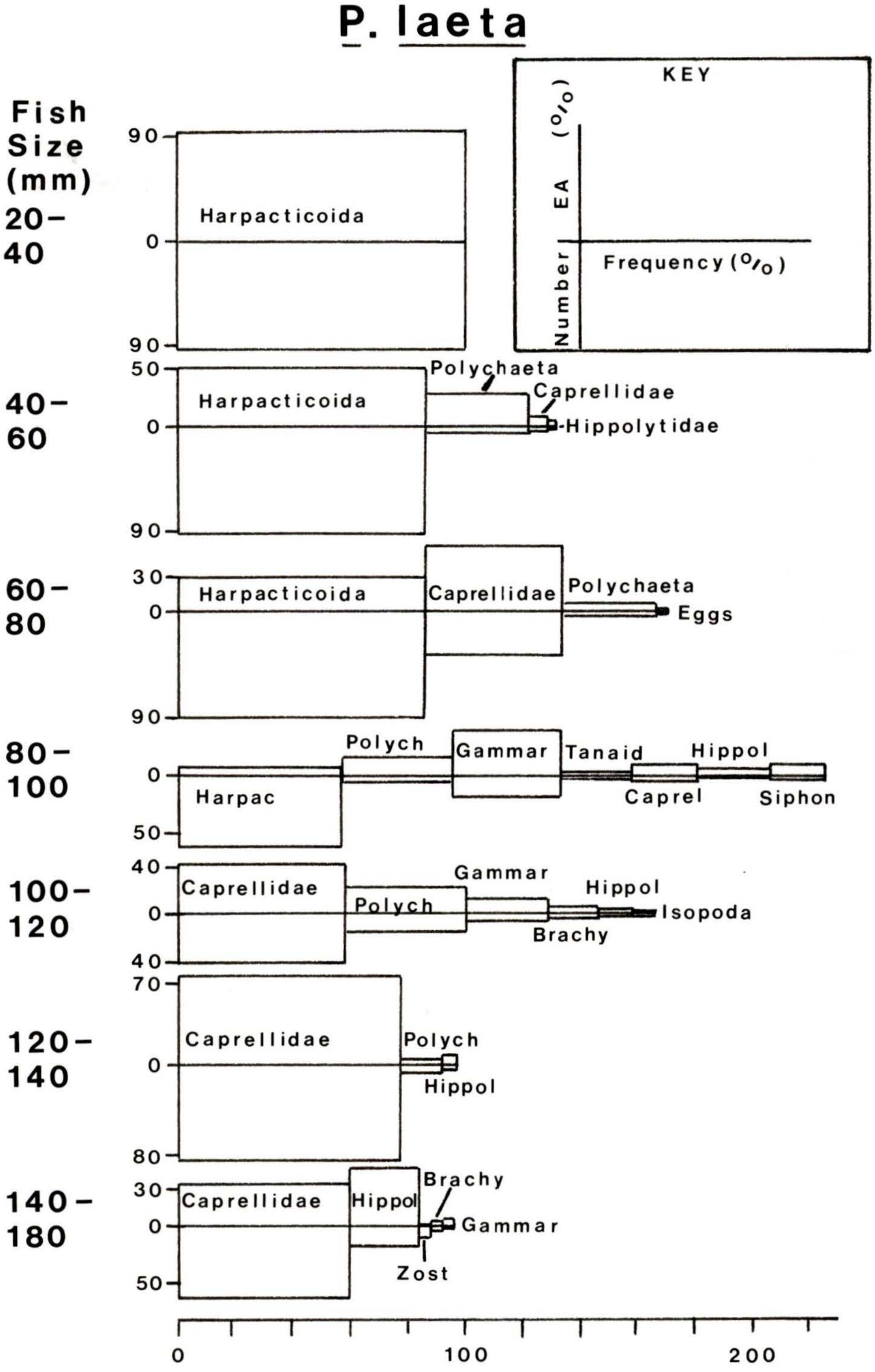

P. laeta
KEY
EA (%)
Number
Frequency (%)
Fish Size (mm)
20-40
90
0
90
Harpacticoida
40-60
50
0
90
Harpacticoida
Polychaeta
Caprellidae
Hippolytidae
60-80
30
0
90
Harpacticoida
Caprellidae
Polychaeta
Eggs
80-100
0
50
Harpac
Polych
Gammar
Tanaid
Caprel
Hippol
Siphon
100-120
40
0
40
Caprellidae
Polych
Gammar
Brachy
Hippol
Isopoda
120-140
70
0
80
Caprellidae
Polych
Hippol
140-180
30
0
50
Caprellidae
Hippol
Brachy
Gammar
Zost
0
100
200

Figure 8. Indexes of relative importance of the prey items in the diet of P. ornata of different size classes showing dietary change with growth. Axes and abbreviations as described in figure 9 with the addition of Cirr = Cirripedia, and tubes referring to areanaceous tubes found in stomachs. Sample sizes as in Table 8.

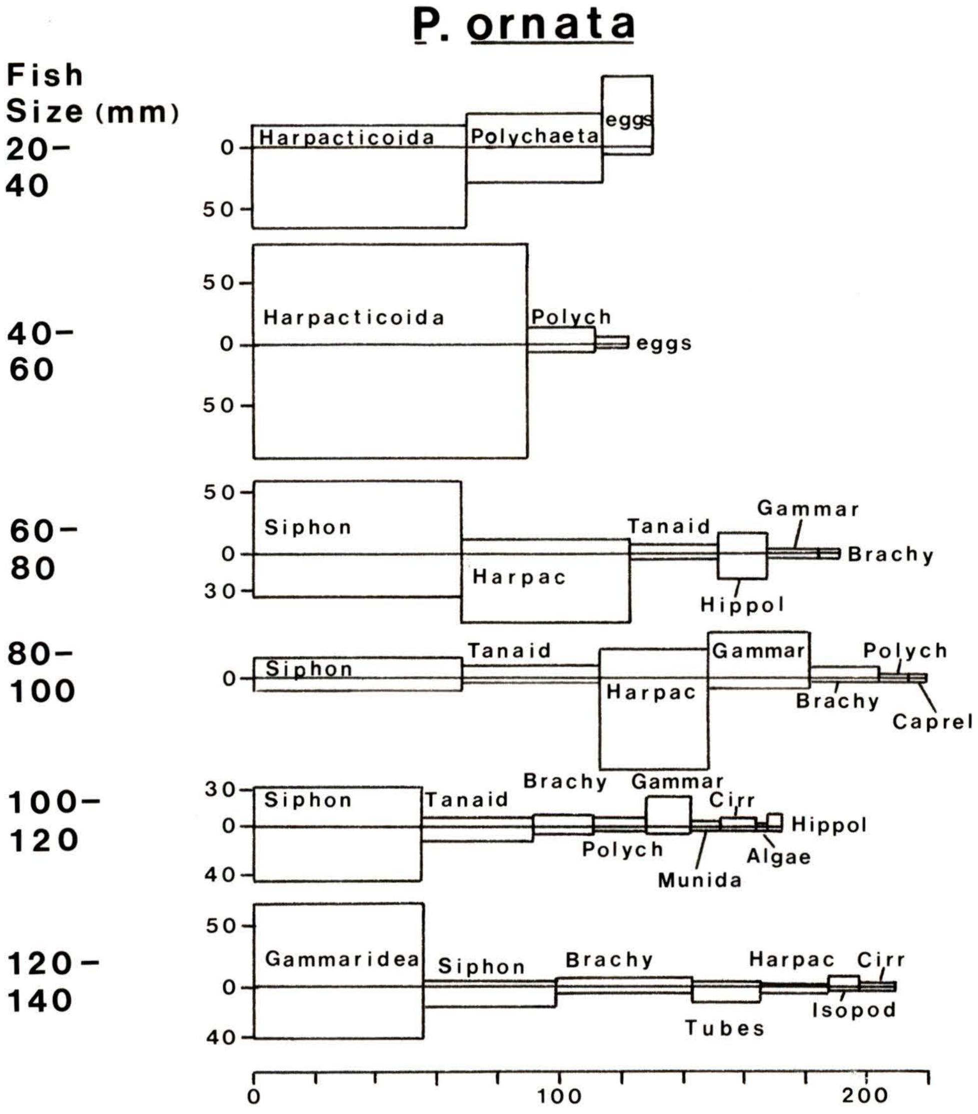

P. ornata
Fish Size (mm)
20–40
0
50
Harpacticoida
Polychaeta
eggs
40–60
50
0
50
Harpacticoida
Polych
eggs
60–80
50
0
30
Siphon
Harpac
Tanaid
Gammar
Brachy
Hippol
80–100
0
Siphon
Tanaid
Harpac
Gammar
Polych
Brachy
Caprel
100–120
30
0
40
Siphon
Tanaid
Brachy
Gammar
Cirr
Hippol
Polych
Munida
Algae
120–140
50
0
40
Gammaridea
Siphon
Brachy
Harpac
Cirr
Tubes
Isopod
0
100
200

Figure 9. Frequency (vertical axis) of the contribution to the diet by siphons or caprellids when either item present, showing marked separation in use of these prey types by *Pholis*. Histograms for *P. laeta* (striped) and *P. ornata* (clear) total 100% of the 51 *P. laeta* and 35 *P. ornata* in the sample.

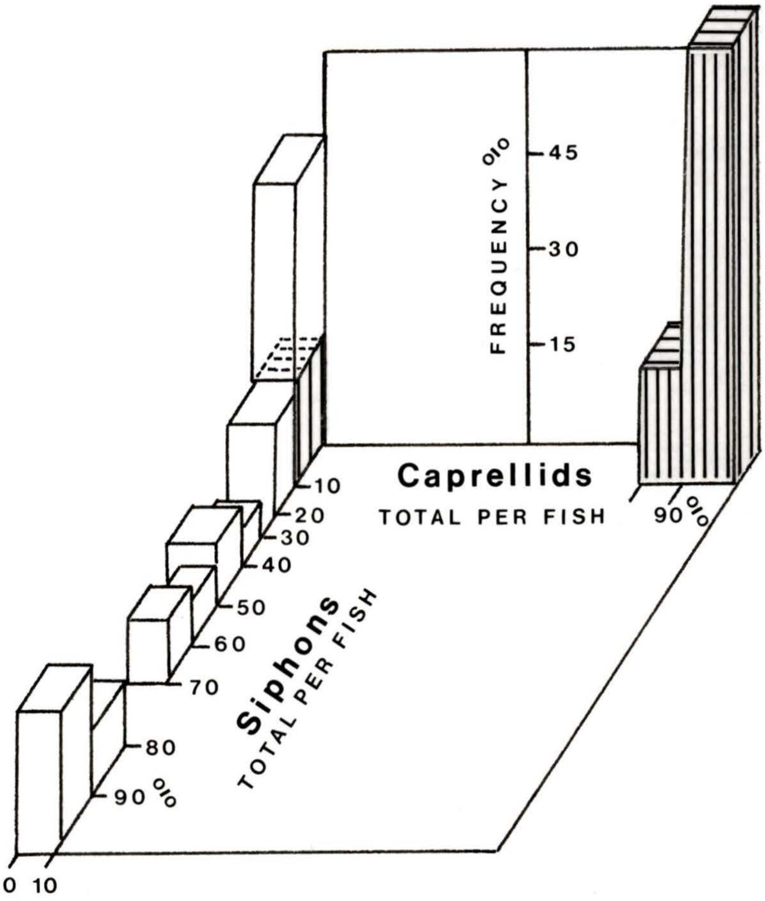

FREQUENCY %
45
30
15
Caprellids
TOTAL PER FISH
90 %
10
20
30
40
50
60
70
80
90 %
Siphons
TOTAL PER FISH
0 10

TABLE 8

SIZE CLASSES OF *PHOLIS* SHOWING WHERE CONCORDANCE BETWEEN INDIVIDUAL FISH OF A SIZE CLASS EXISTED IN PREY TYPES TAKEN

	P. laeta			*P. ornata*		
Fish Size	Concordance	Principal Prey	N	Concordance	Principal prey	N
20-40	$p<0.01$**	copepod	13	$p>0.05$	copepod	14
40-60	$p<0.001$**	copepod	28	$p>0.05$	copepod	10
60-80	$p<0.01$**	copepod	20	$p<0.001$*	siphons	18
80-100	$0.2<p<0.3$	copepod	20	$p<0.001$*	siphons	21
100-120	$p<0.001$**	caprellid	24	$p<0.001$*	siphons	28
120-140	$p<0.001$**	caprellid	22	$0.5<p<0.75$	gammarid	9
140-180	$0.01<p<0.05$*	caprellid	17			

TABLE 9

RANK CORRELATION AND SIGNIFICANCE OF INDEXES OF RELATIVE IMPORTANCE OF *PHOLIS* SIZE CLASS DIETS

	P. laeta 20-40	*P. laeta* 40-60	*P. laeta* 60-80	*P. laeta* 80-100	*P. laeta* 100-120	*P. laeta* 120-140	*P. laeta* 140-180	*P. ornata* 20-40	*P. ornata* 40-60	*P. ornata* 60-80	*P. ornata* 80-100	*P. ornata* 100-120	*P. ornata* 120-140
P. laeta 20-40	X												
P. laeta 40-60	0.53*	X											
P. laeta 60-80	0.53*	0.72*	X										
P. laeta 80-100	0.43*	0.67*	0.46*	X									
P. laeta 100-120	-0.21	0.39	0.24	0.33	X								
P. laeta 120-140	-0.14	0.69*	0.47*	0.40*	0.67*	X							
P. laeta 140-180	-0.19	0.22	-0.02	0.15	0.50*	0.45*	X						
P. ornata 20-40	0.60*	0.57*	0.79*	0.36	-0.02	0.14	-0.34	X					
P. ornata 40-60	0.60*	0.57*	0.79*	0.36	-0.02	0.14	-0.34	1.00*	X				
P. ornata 60-80	0.38	0.17	-0.07	0.50*	-0.08	-0.11	0.05	0.02	0.02	X			
P. ornata 80-100	0.43*	0.27	0.27	0.65*	0.14	-0.02	-0.03	0.22	0.22	0.65*	X		
P. ornata 100-120	-0.28	-0.28	-0.38	0.15	0.03	-0.15	-0.09	-0.24	-0.24	0.41*	0.45	X	
P. ornata 120-140	0.10	-0.26	-0.26	0.09	0.06	-0.42	-0.08	-0.18	-0.18	0.33	0.33	0.33	X

* sig. < 0.05

Figure 10. Correlation between diets of *P. laeta* and *P. ornata* (solid squares) and of *P. laeta* (solid circles) and *P. ornata* (open circles) showing the lowering of similarity with increasing difference in size of fish both within and between species. Size differences calculated from midpoint of size class. Sample sizes as in Table 8.

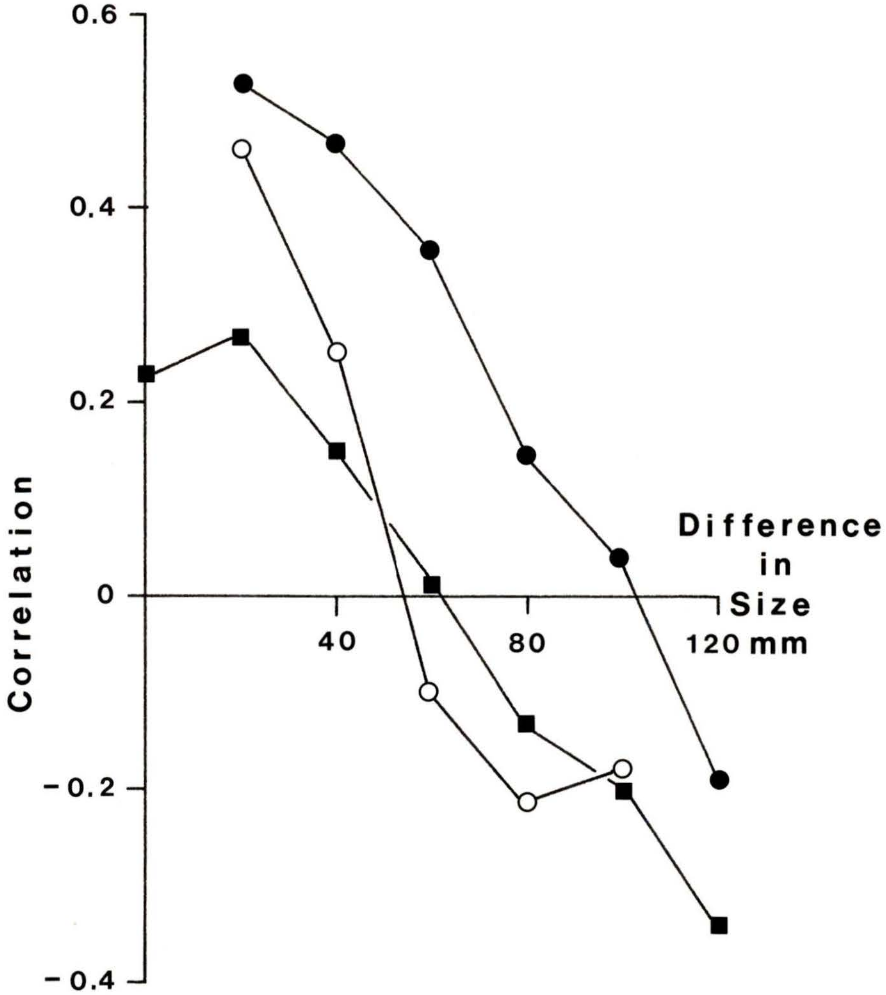

0.6
0.4
0.2
0
-0.2
-0.4
Correlation
40
80
120 mm
Difference
in
Size

Figure 11. Diet diversity of P. laeta (solid circle) and P. ornata (open circles) based on number of prey in each prey type showing general trend for increased diversity with growth. Sample sizes as in Table 8.

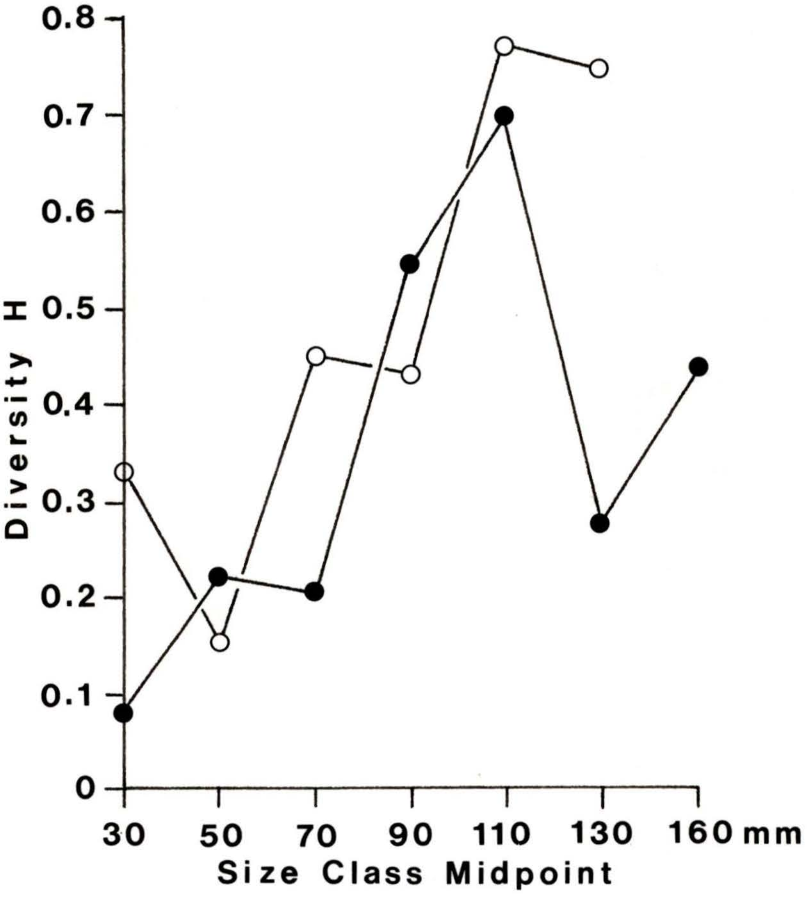

0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Diversity H
30
50
70
90
110
130
160 mm
Size Class Midpoint

TABLE 10

PHOLIS LAETA STANDARDIZED MATRIX OF FOOD USE BY AGE, SHOWING NICHE WIDTH, AND OVERLAP IN FOOD TYPE

Age	N	Copepod	Polychaete	Caprellid	Shrimp	Siphon	Amphipod	Crab
0	63	28	5	10	1	0	0	0
1	45	1	9	14	3	3	13	1
2,2+	39	0	1	6	4	0	1	0

Niche Width Parameters*		Niche Overlap Parameters*	
H_A	$= 0.404$	H_B	$= 0.661$
$\Sigma u_i h_i(b)$	$= 0.473$	$\Sigma v_j h_j(a)$	$= 0.216$
H_T	$= 0.877$	H_T	$= 0.877$
$\frac{H_A}{H_T}$	$= 0.461$	$\frac{H_B}{H_T}$	$= 0.754$
$\frac{\Sigma u_i h_i(b)}{H_T}$	$= 0.539$	$\frac{\Sigma v_j h_j(a)}{H_T}$	$= 0.246$

where H_T (total diversity) = H_A(age group diversity) + $\Sigma u_i h_i(b)$ = H_B (food type diversity) + $\Sigma v_j h_j(a)$

---

* see text and Pielou (1972) for additional details

TABLE 11

PHOLIS ORNATA STANDARDIZED MATRIX OF FOOD USE BY AGE, SHOWING NICHE WIDTH, AND OVERLAP IN FOOD TYPE

Age	N	Copepod	Polychaete	Eggs	Siphons	Shrimp	Tanaid	Amphipod	Crab	*Munida*	Barnacle	Algae
0	42	22	8	12	12	4	1	1	1	0	0	0
1	50	4	2	0	9	2	3	12	4	1	1	1
2	9	0	0	0	0	0	0	2	0	0	0	0

Niche Width Parameters*

$H_A = 0.310$

$\Sigma u_i h_i(b) = 0.659$

$H_T = 0.969$

$\frac{H_A}{H_T} = 0.320$

$\frac{\Sigma u_i h_i(b)}{H_T} = 0.680$

Niche Overlap Parameters*

$H_B = 0.804$

$\Sigma v_j h_j(a) = 0.165$

$H_T = 0.969$

$\frac{H_B}{H_T} = 0.830$

$\frac{\Sigma v_j h_j(a)}{H_T} = 0.170$

---

* legend as in Table 10, text, and Pielou (1972)

TABLE 12

OVERLAP OF FOOD TYPES TAKEN BY *P. LAETA* AND *P. ORNATA* GROUPED INTO 20 mm SIZE GROUPS

	P. laeta 20-40	*P. laeta* 40-60	*P. laeta* 60-80	*P. laeta* 80-100	*P. laeta* 100-120	*P. laeta* 120-140	*P. laeta* 140-180	*P. ornata* 20-40	*P. ornata* 40-60	*P. ornata* 60-80	*P. ornata* 80-100	*P. ornata* 100-120	*P. ornata* 120-140
P. laeta 20-40	1												
P. laeta 40-60	0.845	1											
P. laeta 60-80	0.475	0.618	1										
P. laeta 80-100	0.192	0.400	0.338	1									
P. laeta 100-120	0.033	0.413	0.794	0.573	1								
P. laeta 120-140	0.009	0.248	0.874	0.288	0.867	1							
P. laeta 140-180	0.001	0.198	0.482	0.352	0.584	0.666	1						
P. ornata 20-40	0.246	0.425	0.223	0.244	0.237	0.067	0.018	1					
P. ornata 40-60	0.969	0.912	0.259	0.264	0.113	0.077	0.022	0.375	1				
P. ornata 60-80	0.175	0.264	0.092	0.347	0.088	0.048	0.254	0.050	0.172	1			
P. ornata 80-100	0.458	0.467	0.073	0.878	0.324	0.080	0.127	0.137	0.459	0.432	1		
P. ornata 100-120	0.031	0.216	0.120	0.721	0.280	0.170	0.234	0.143	0.154	0.669	0.656	1	
P. ornata 120-140	0.026	0.110	0.040	0.858	0.383	0.034	0.099	0.028	0.048	0.075	0.809	0.152	1

Figure 12. Graphical representation of overlap in food type taken by _P. laeta_ with _P. laeta_ (solid circles and _P. ornata_ (open circles) throughout size ranges. Overlaps of identically sized intraspecific groups assigned the value of 1. Sample sizes as in Table 8.

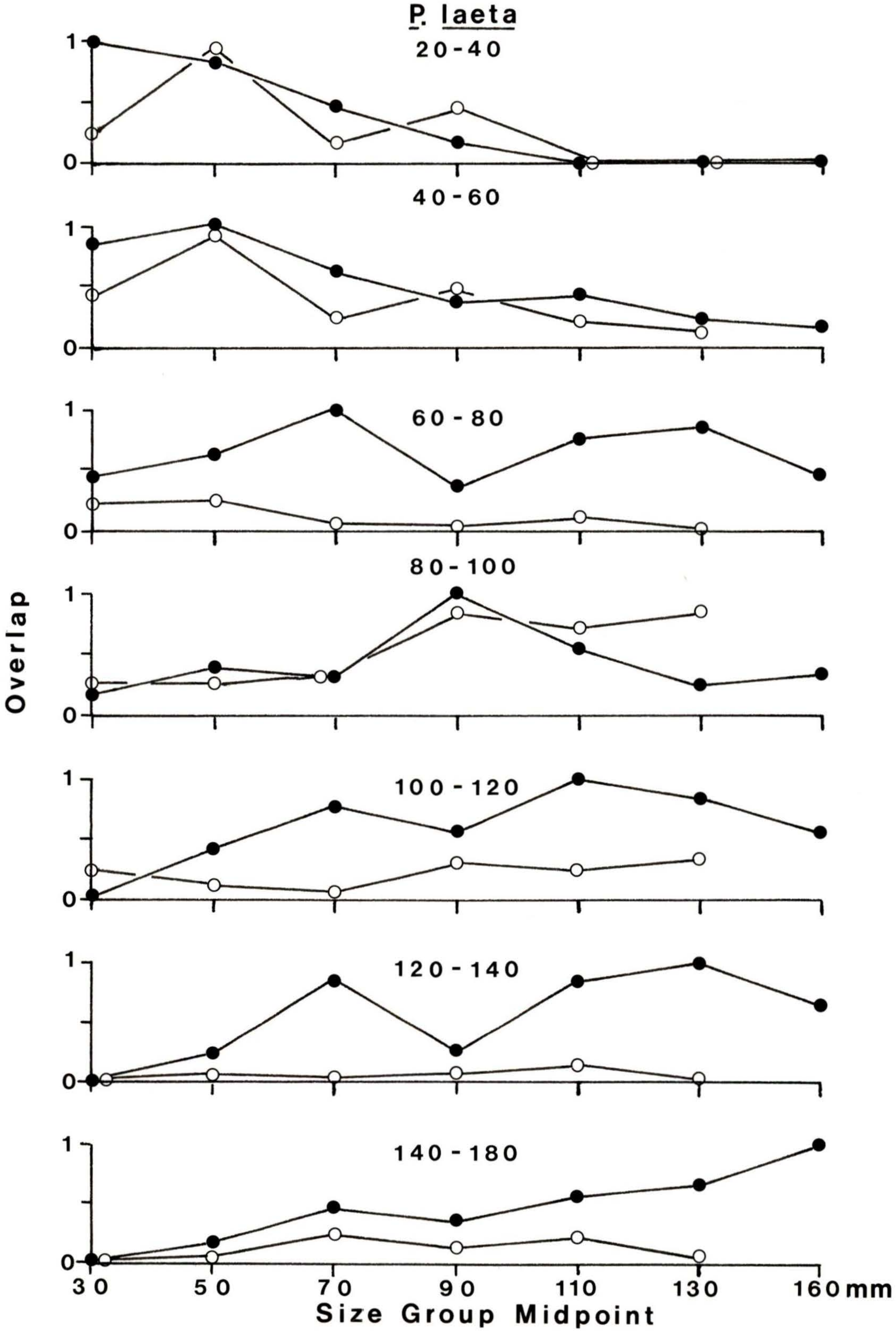
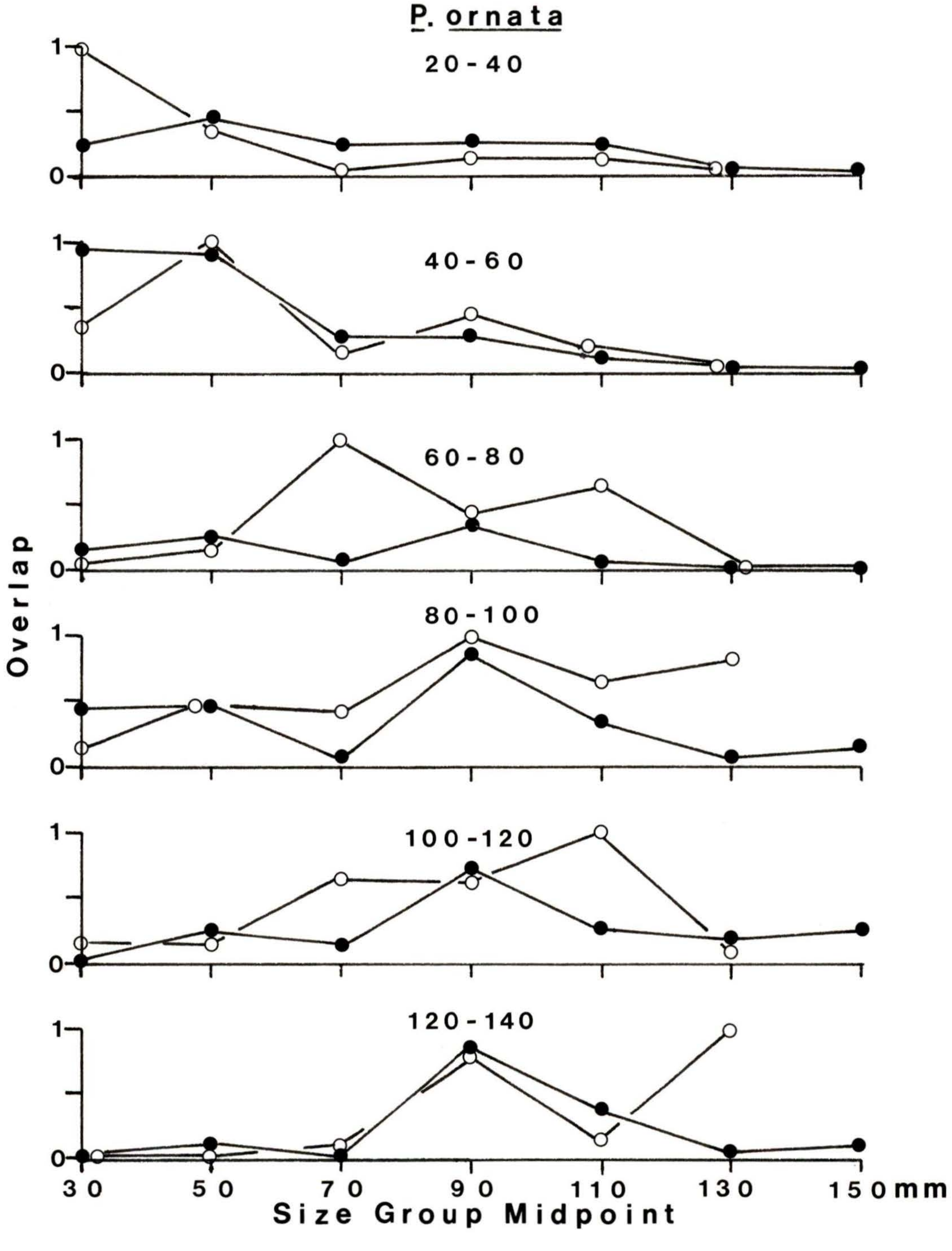

P. laeta
20-40
40-60
60-80
80-100
100-120
120-140
140-180
Overlap
1
0
30
50
70
90
110
130
160mm
Size Group Midpoint

Figure 13. Graphical representation of overlap in food type taken by P. *ornata* throughout size ranges. Coding as in figure 14. Sample sizes as in Table 8.


P. ornata
20 - 40
40 - 60
60 - 80
80 - 100
100 - 120
120 - 140
Overlap
1
0
30
50
70
90
110
130
150 mm
Size Group Midpoint

Principal component analysis resolves the fish into three major groupings based on diet; small size fish of both species, large *P. laeta* and large *P. ornata* respectively (Figure 14). Two factors account for 85% of the variation (Table 13).

Food Size

Size of food taken increases with body size but does not differ significantly between the species (Figures 15, 16; Table 14). Overlaps in food size taken decrease somewhat with increasing size difference but are usually high between identically sized *P. laeta* and *P. ornata* (Table 15). The resource utilization curves (Figure 17) and mean niche location based on food size are similar (Table 16) although niche breadth based on food size is larger in *P. laeta* than *P. ornata* using the method of Roughgarden (1974). However, niche breadth of food sizes taken by *P. ornata* are higher than *P. laeta* when computed using Levin's (1968) formula.

Activity Patterns

Laboratory Analysis

Activity was not evenly distributed throughout the 24 hour periods tested (Table 17) and the patterns that were evident in both species under both experimental conditions (Figures 18, 19) were significantly correlated on most runs (Table 18). Correlation was less likely under constant dark conditions than under photoperiod conditions. Peak activity under photoperiod conditions coincided with dusk and dawn. Under constant dark conditions, only a pronounced peak at the time of anticipated dawn was evident.

Figure 14. Graphical representation of rotated factor scores of diet indexes of relative importance showing high loading of small fish on factor 1, high loading of large *P. laeta* (solid circles) on factor 2, and low loading of large *P. ornata* (hollow circles). Based on sample sizes in Table 8.

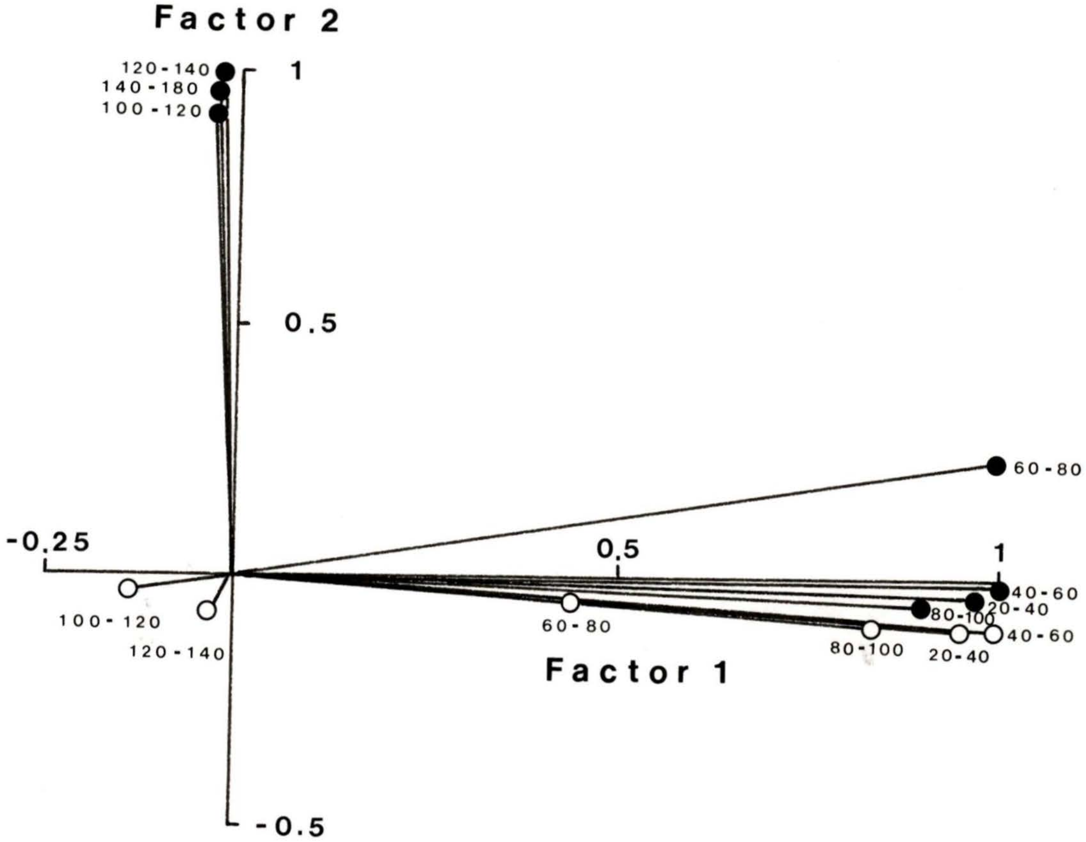

Factor 2
1
0.5
-0.5
-0.25
0.5
1
Factor 1
120-140
140-180
100-120
60-80
40-60
20-40
80-100
100-120
120-140
60-80
80-100
20-40
40-60

TABLE 13

UNROTATED FACTOR SCORES FOR *PHOLIS* SIZE GROUPS FROM ORDINATION OF DIET

Species Size(mm)	Factor1(58.7% of variance)	Factor 2 (26.7% of variance)	Factor 3 (14.6% of variance)
P. laeta			
20-40	0.98476	0.06168	-0.12769
40-60	0.98606	0.07388	-0.14376
60-80	0.93012	0.32953	-0.06522
80-100	0.89717	0.06228	0.00071
100-120	-0.12007	0.92898	0.18015
120-140	-0.11931	0.95636	0.22063
140-180	-0.14602	0.94295	0.20002
P. ornata			
20-40	0.90872	0.06617	-0.20391
40-60	0.98524	0.05989	-0.13992
60-80	0.55965	-0.21931	0.69603
80-100	0.88563	-0.13273	0.35189
100-120	0.02452	-0.31723	0.87104
120-140	0.02582	-0.14324	0.20579

Figure 15. Size of food taken by *Pholis* showing increases with fish size. Depicted as mean ± 95% confidence intervals for *P. ornata* (open circles) and *P. laeta* (solid circles). Sample sizes noted on graph.

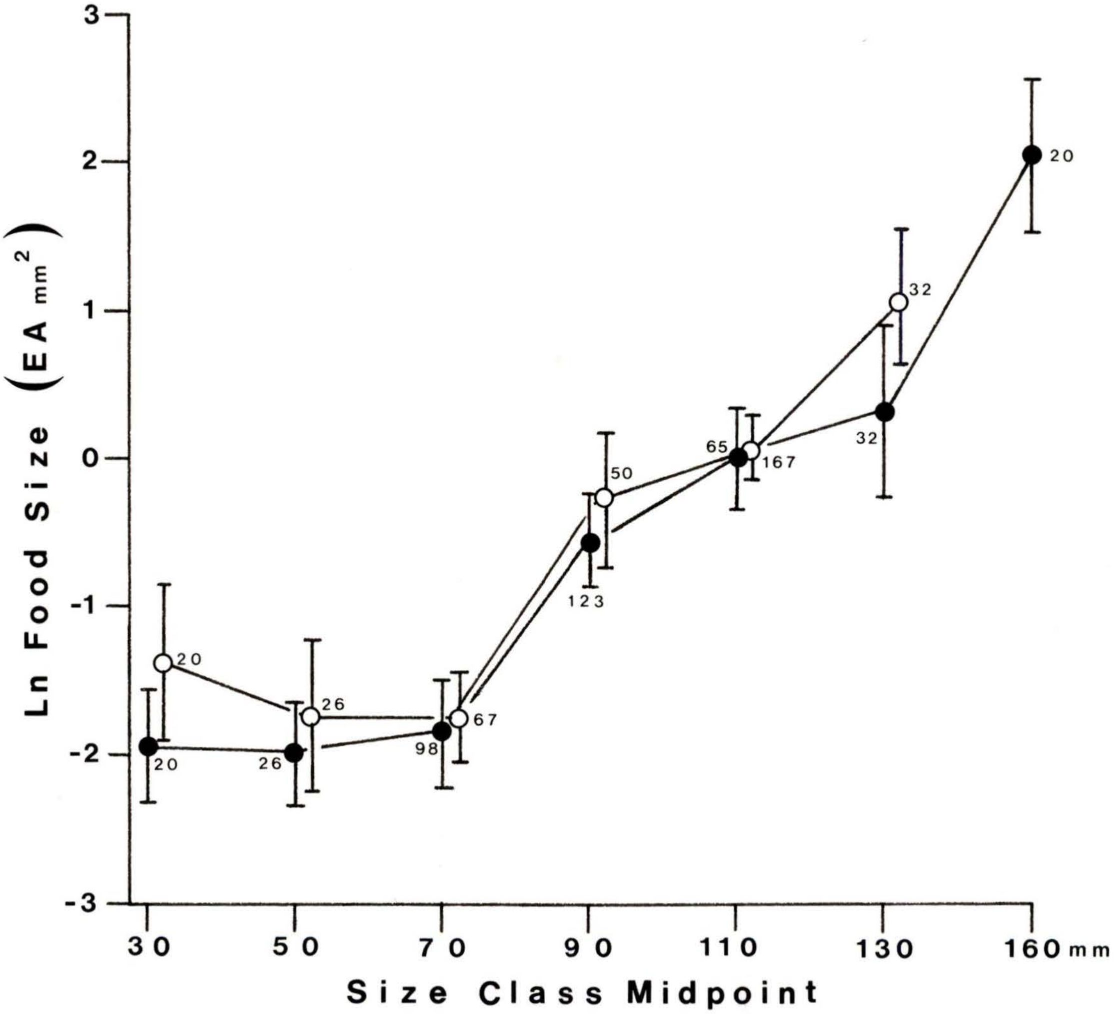

3
2
1
0
-1
-2
-3
Ln Food Size (EA $_{\mathrm{mm}^2}$)
20
20
26
26
98
67
123
50
65
167
32
32
20
30
50
70
90
110
130
160 mm
Size Class Midpoint

Figure 16. A comparison of size groups of *P. laeta* and *P. ornata* showing a connection by lines where prey size was not significantly different. Based on sample sizes in Figure 15.

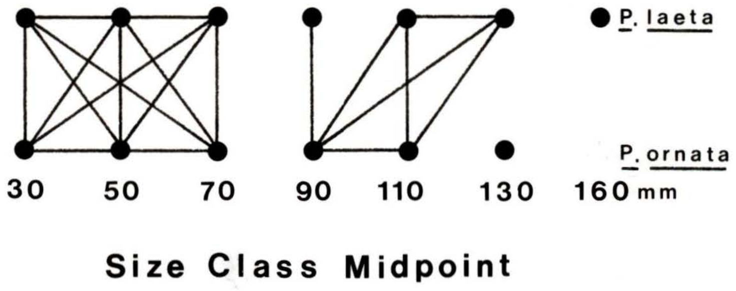

P. laeta
P. ornata
30
50
70
90
110
130
160 mm
Size Class Midpoint

TABLE 14

ANALYSIS OF VARIANCE OF FOOD SIZES TAKEN BY PHOLIS GREATER THAN 80 mm SL SHOWING FOOD SIZE VARIES WITH FISH SIZE IN BOTH SPECIES

Source	SS	DF	MS	F	SIG
MAIN EFFECTS	161.194	4	40.298	18.498	<0.001**
Species	7.304	1	7.304	3.353	0.068 NS
Fish Size	155.481	3	51.827	23.790	<0.001**
INTERACTION					
Species x Fish Size	5.481	2	2.740	1.258	0.258 NS

TABLE 15

OVERLAP IN FOOD SIZE TAKEN BY VARIOUS SIZE GROUPS OF *PHOLIS*

	P. laeta			*P. ornata*		
	20-80 mm	80-120 mm	>120 mm	20-80 mm	80-120 mm	>120 mm
P. laeta 20-80 mm	X					
P. laeta 80-120 mm	0.88	X				
P. laeta >120 mm	0.89	0.95	X			
P. ornata 20-80 mm	1.00	0.91	0.91	X		
P. ornata 80-120 mm	0.80	0.98	0.92	0.85	X	
P. ornata >120 mm	0.14	0.59	0.48	0.21	0.67	X

Figure 17. Food size resource utilization histograms of the species showing similarity between *P. laeta* and *P. ornata* based on sample sizes in Figure 15. Contributions of <1% of resource use were not plotted although they were included in the calculations for this figure and Table 16. Total area under histograms totals 100% of the food sizes used by each species accounting for the range of prey sizes taken, the amount of food taken on average by the fish of a particular size class and the relative abundances of the size classes in the censused populations.

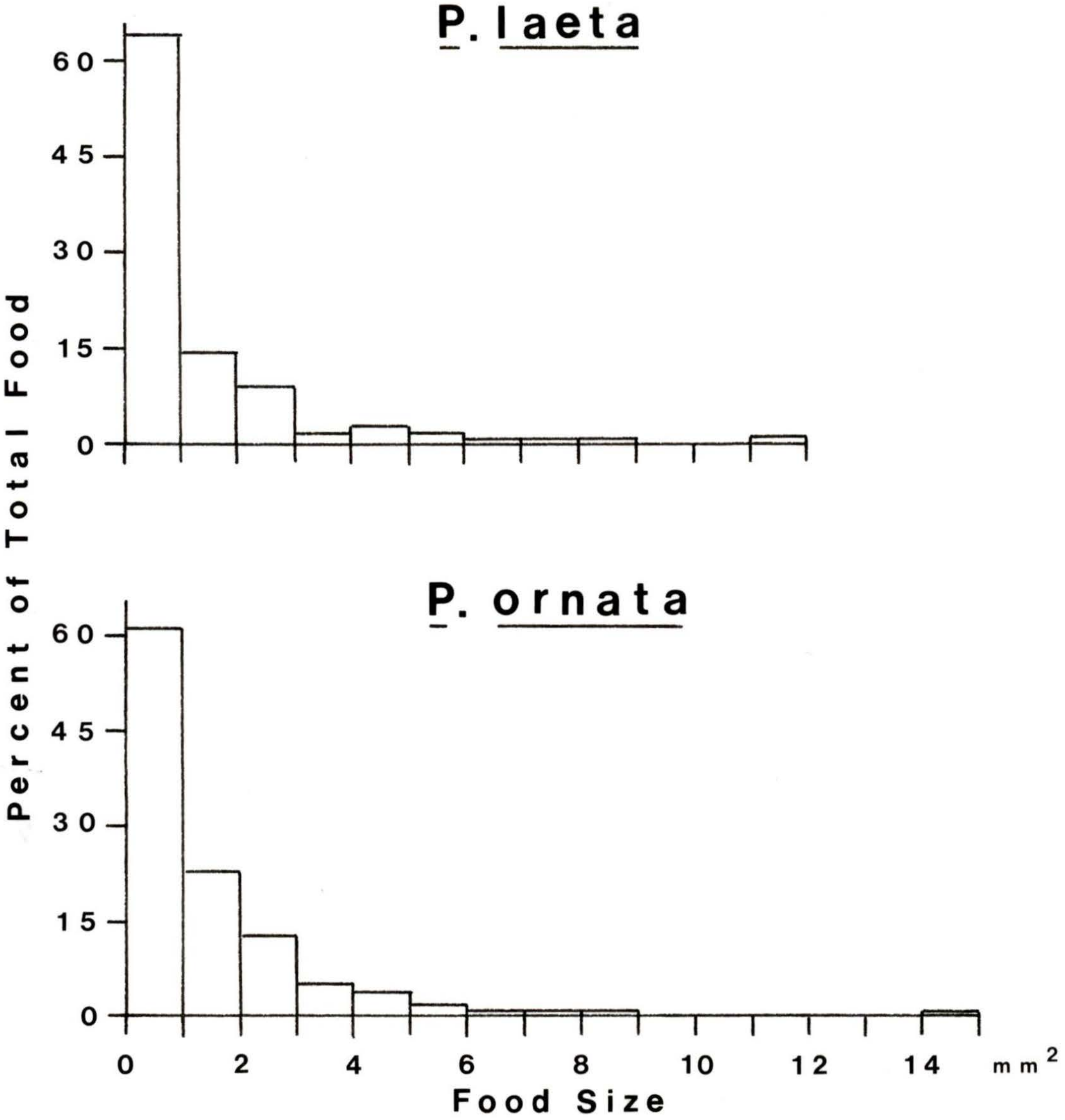

P. laeta
P. ornata
Percent of Total Food
60
45
30
15
0
0
2
4
6
8
10
12
14
mm^2
Food Size

TABLE 16

FOOD SIZE NICHE PARAMETERS OF *P. LAETA* AND *P. ORNATA*

	Age	Size	Average EA	Variance $(EA)^2$	Mean Food Total ($\bar{X}$) (EA)	Proportion of Sample (p_1)	Adjusted Proportion ($P_1{}^1$)
P. laeta	0	<80 mm	0.19	0.79	313	0.791	0.451
	1	80-120	2.43	27.74	1915	0.127	0.443
	2,2+	>120	6.14	164.32	714	0.082	0.107
P. ornata	0	<80	0.51	2.98	411	0.875	0.606
	1	80-120	2.53	25.34	1931	0.114	0.371
	2	>120	6.10	85.58	1269	0.011	0.024

	Mean Niche Location (EA)	Niche Width $(EA)^2$	Within Phenotype Component (%)	Between Phenotype Component (%)
P. laeta	1.8	33.5	90	10
P. ornata	1.4	14.7	90	10

TABLE 17

GOODNESS OF FIT OF MEAN ACTIVITY TO AN EVEN DISTRIBUTION

	Maximum $\lvert d_i \rvert$*	N	D**	Probability
Pholis laeta				
Photoperiod	23.3	12	1.94	<0.001**
Constant Dark	33.5	12	2.79	<0.001**
Pholis ornata				
Photoperiod	32.3	12	2.69	<0.001**
Constant Dark	24.2	12	2.02	<0.001**

* Kolmogorov-Smirnov d_i: the absolute difference between the cumulative frequency of percent activity observed and that expected if activity was evenly distributed.

** $D = \max \lvert d_i \rvert \div$ number of 2 hour activity groups

Figure 18. Laboratory activity patterns (mean ± standard error) under natural photoperiod conditions showing similar distribution of total activity by *P. laeta* (solid circles) and *P. ornata* (open circles) and a marked peak at dawn and dusk based on 10 fish of each species.

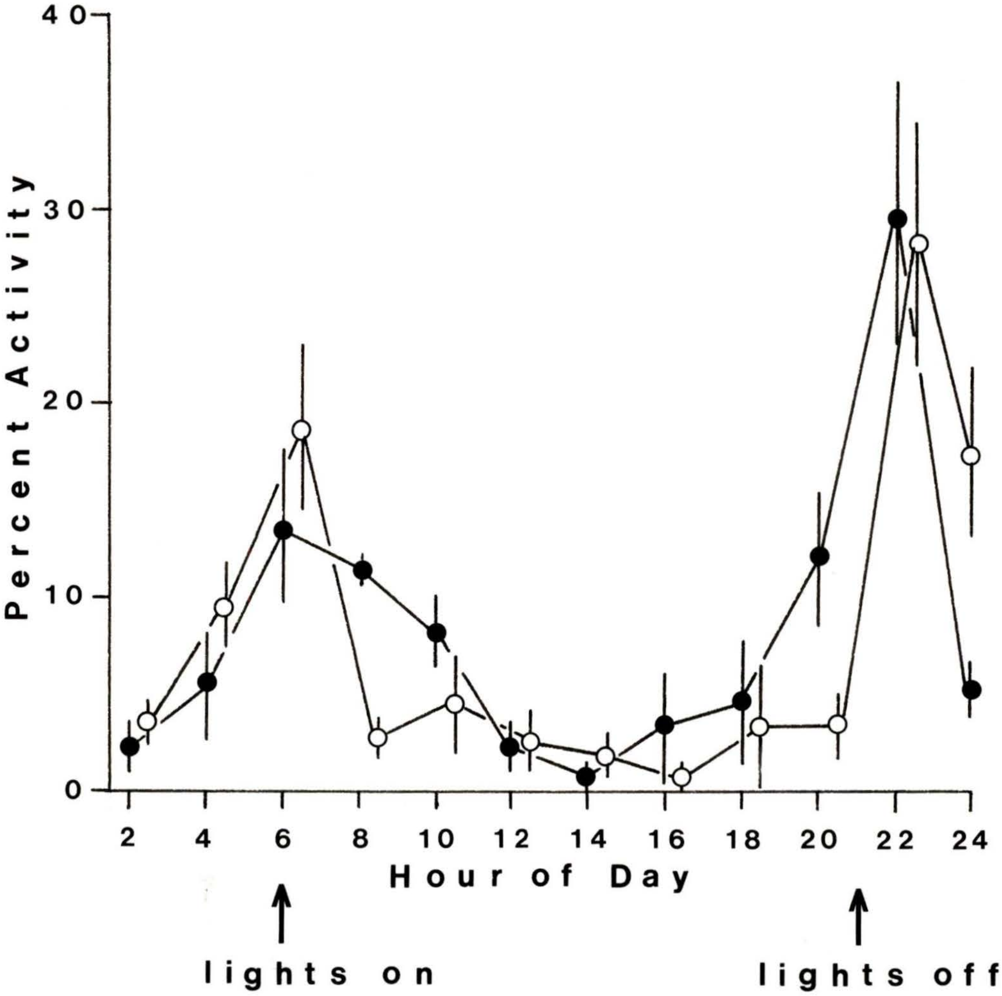

Percent Activity
0
10
20
30
40
Hour of Day
2
4
6
8
10
12
14
16
18
20
22
24
lights on
lights off

Figure 19. Laboratory activity patterns (mean ± standard error) under constant dark conditions showing similarity between *P. laeta* (solid circles) and *P. ornata* (hollow circles) based on 12 fish of each species.

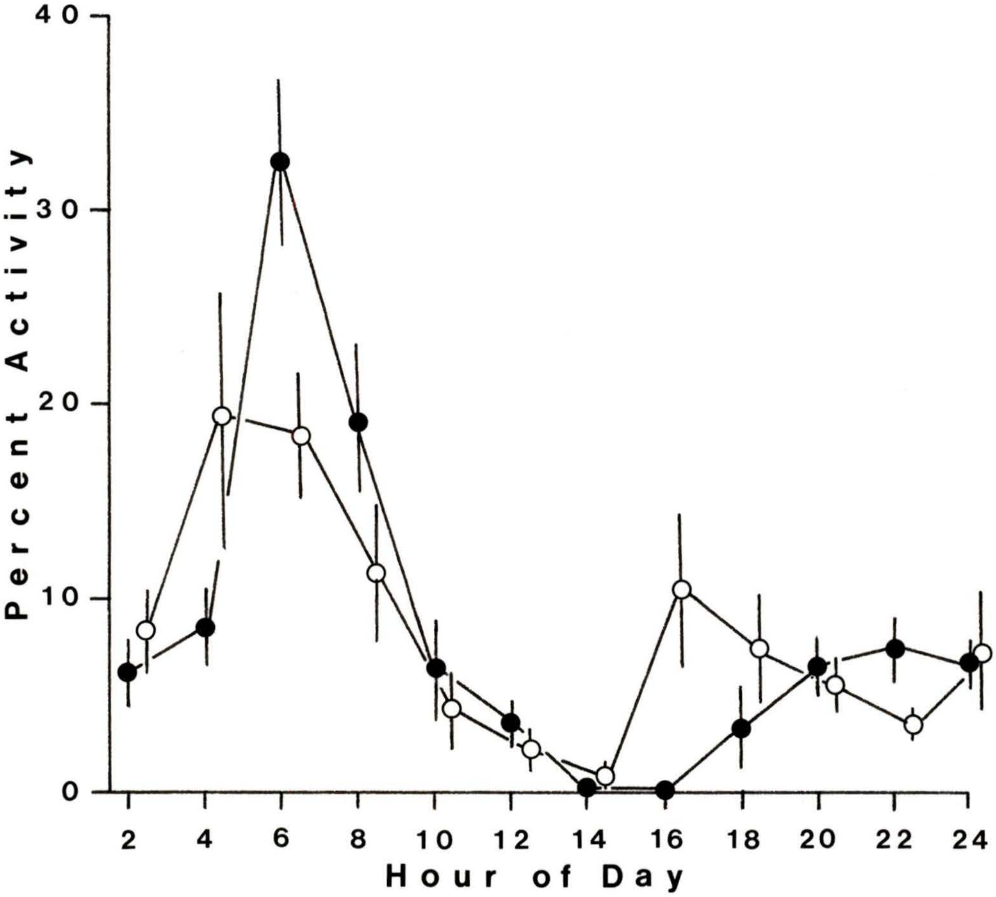

Percent Activity
40
30
20
10
0
2
4
6
8
10
12
14
16
18
20
22
24
Hour of Day

TABLE 18

SUMMARY OF CORRELATION OF _P. LAETA_ ACTIVITY WITH _P. ORNATA_

Regime	Run Number	Correlation Coeff.	Ho: rankings of activity are different* Prob.
Dark			
	1	0.5828	0.001*
	2	0.1450	0.225 NS
	3	0.1600	0.238 NS
	4	-0.0797	0.369 NS
	5	0.2388	0.148 NS
	6	0.4129	0.025 *
	OVERALL	0.5394	0.035*
Photoperiod			
	1	0.7782	0.001*
	2	0.3113	0.074 NS
	3	0.5387	0.002*
	4	0.3448	0.049*
	5	0.5494	0.001*
	OVERALL	0.6853	0.007*

* coding: NS - not significantly correlated

* - significantly correlated at $\alpha = 0.05$

Overlap under photoperiod (0.89) and constant dark (0.84) conditions were high. P. laeta niche breadth of activity was higher than P. ornata under photoperiod conditions (6.75 versus 6.22) but lower (5.76 versus 8.34) under constant dark (Table 2).

Field Evidence for Time of Feeding

Both species had a higher mean amount of food in the stomach when captured at mid-morning than during darkness when tide conditions were identical (Figure 20). Food totals are averaged for the whole size range of specimens captured but, as expected, the size ranges of both species captured during the day and at night were similar (Figures 21 and 22).

Life History

Length Frequencies

Length frequency histograms of P. laeta (Figure 23) and P. ornata (Figure 24) show peaks characteristic of at least 3 separate size groupings for P. laeta and 2 for P. ornata. Many P. laeta grew larger than the largest sized P. ornata captured in this study.

Otolith Analysis

Based on otolith analysis, P. laeta (Table 19) grew to an average length of 81.4 mm at the time of first annulus formation, 123.3 mm SL by the end of the second year, and up to 147.7 mm SL by June of their third year. One specimen 159.1 mm SL had 6 annuli.

Figure 20. Histograms showing that Pholis average more food in stomach during the day than at night depicted as mean ± 95% confidence interval. Numbers within histograms are percent of empty stomachs. Data based on P. laeta (day N = 73, night N = 33) and P. ornata (day N = 43, night N = 36).

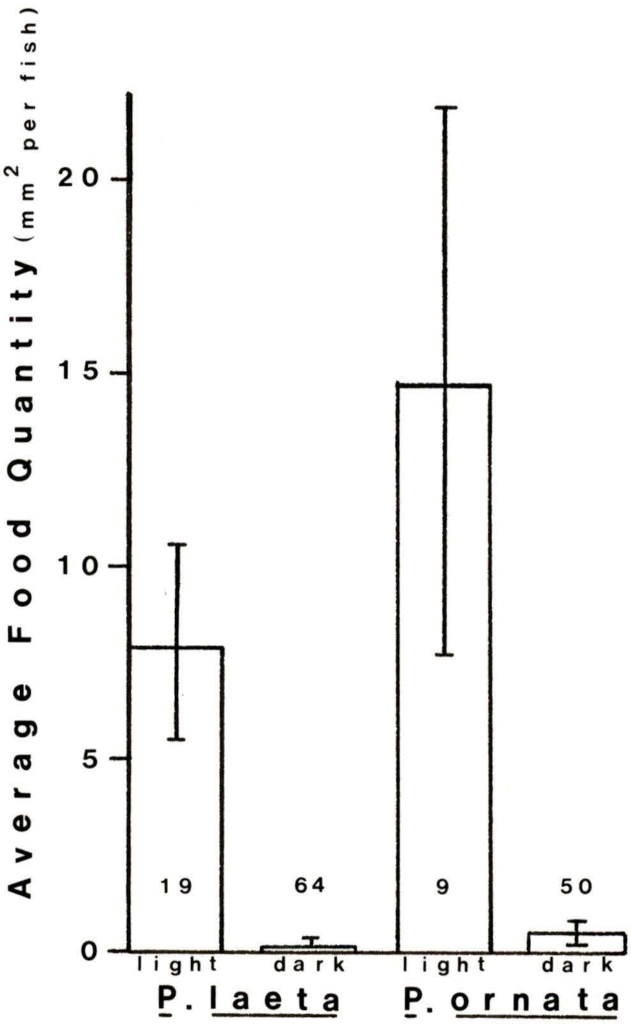

Average Food Quantity (mm^2 per fish)
20
15
10
5
0
19
64
9
50
light
dark
light
dark
P. laeta
P. ornata

Figure 21. Size ranges of _P. laeta_ captured during the day (squares) and at night (triangles). Sample sizes as in Figure 20.

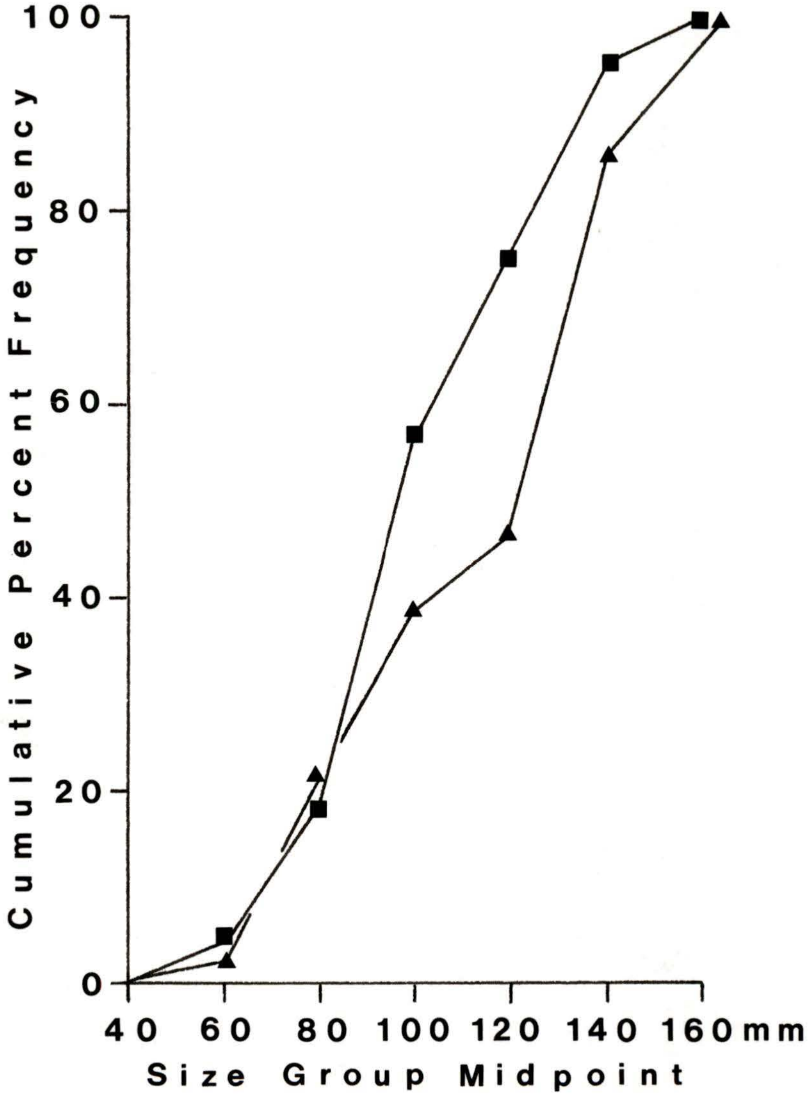

Cumulative Percent Frequency
100
80
60
40
20
0
40
60
80
100
120
140
160mm
Size Group Midpoint

Figure 22. Size ranges of P. ornata captured during the day (squares) and at night (triangles). Sample sizes as in Figure 20.

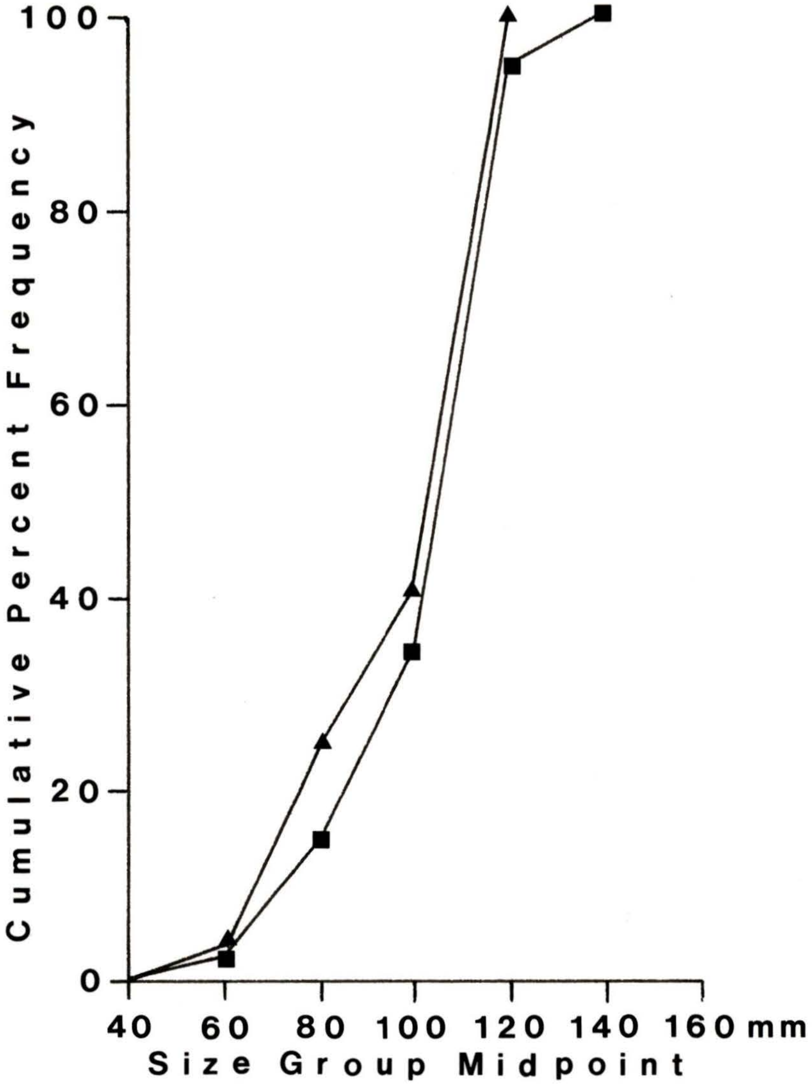

Cumulative Percent Frequency
0
20
40
60
80
100
40
60
80
100
120
140
160 mm
Size Group Midpoint

Figure 23. Length frequencies of *P. laeta* captured in Saanich Inlet during 1980. Arrows point to where histograms were subdivided for growth analysis. Dark areas show standard lengths of mature fish during January. Sample sizes noted on graph.

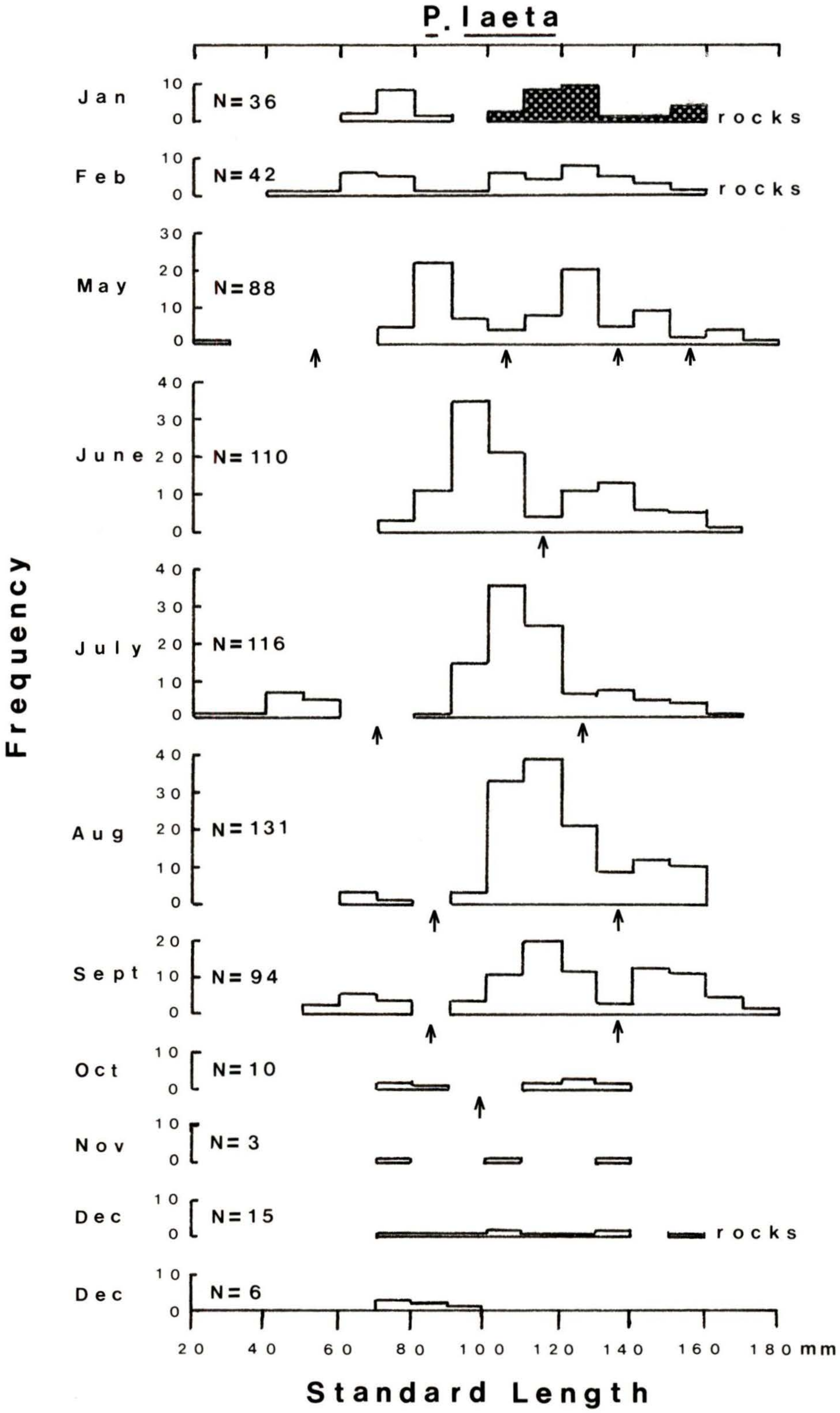

P. laeta
Jan
N=36
rocks
Feb
N=42
rocks
May
N=88
June
N=110
July
N=116
Aug
N=131
Sept
N=94
Oct
N=10
Nov
N=3
Dec
N=15
rocks
Dec
N=6
0
10
20
30
40
20
40
60
80
100
120
140
160
180 mm
Frequency
Standard Length

Figure 24. Length frequencies of *P. ornata* captured in Saanich Inlet during 1980. Arrows point to where lengths were subdivided for growth analysis. Sample sizes noted on graph.

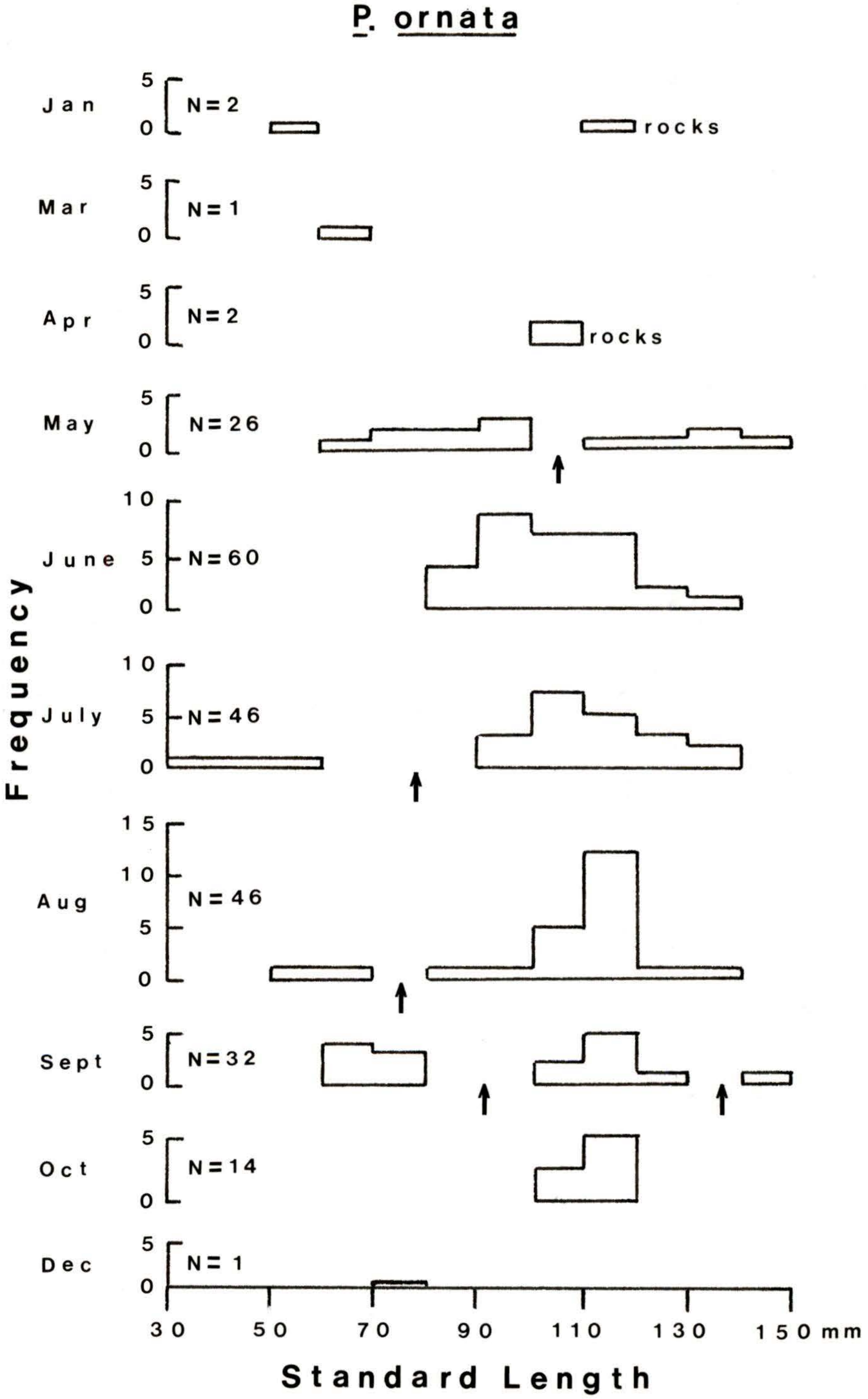

P. ornata
Jan
N = 2
rocks
Mar
N = 1
Apr
N = 2
rocks
May
N = 26
June
N = 60
July
N = 46
Aug
N = 46
Sept
N = 32
Oct
N = 14
Dec
N = 1
0
5
10
15
Frequency
30
50
70
90
110
130
150 mm
Standard Length

TABLE 19

PHOLIS LAETA OTOLITH ANALYSIS

Formula* for calculating lengths at time of annulus formation from Everhart *et al.* (1975):

$$L = -0.16 + \frac{SL + 0.16}{R_o} Ra$$

	Mean (mm)	CI (mm)	Number of specimens
Backcalculated length at first annulus formation	81.4	78.0-84.5	20
Length of one year olds in June 1980	102.1	100.7-103.5	20
Backcalculated length at second annulus formation	123.3	116.5-130.0	4
Length of two year olds in June 1980	135.8	129.0-142.6	4

* where L = backcalculated length

SL = standard length of fish

R_o = otolith diameter

Ra = distance from focus to annulus

-0.16 = regression intercept of otolith size at formation

CI = 95% confidence interval

P. ornata (Table 20) grew to 79.7 mm SL at time of first annulus formation, with specimens up to 116.7 mm being in their second year in June of 1980.

These mean lengths per age class were used to assign ages to sections of the length frequency histograms.

Growth Rates

Age classes of P. laeta and P. ornata showed similar growth rates (Figures 25, 26). The mean sizes at annulus formation at the end of the first and second years (for P. laeta) and the first year for P. ornata, were intermediate between the sizes of the younger cohort in the fall and the older cohort in the spring. This implies the growth of cohorts has not changed radically in the last 3 years for P. laeta or 2 years for P. ornata. Growth was generally faster in the summer than in the winter and in smaller fish based upon the groupings of samples where lengths were not significantly different (Table 21).

Estimation of Number of Young in the Year

The catch curves for P. laeta and P. ornata are similar with fitted logarithmic slopes of -0.80 for P. laeta and -0.87 for P. ornata (Figure 27). Based on the average number of one year old P. laeta captured (64.2), an average of 405 young of the year P. laeta were presumed to be present in sample area. Similarly, from an average capture of 10.3, 1 year old P. ornata, 75 young P. ornata were estimated to occur in the region.

TABLE 20

PHOLIS ORNATA OTOLITH ANALYSIS

Formula* for calculating lengths at time of annulus formation from Everhart *et al.* (1975):

$$L = 0.16 + \frac{SL - 0.16}{R_o} Ra$$

	Mean (mm)	CI (mm)	Number of Specimens
Backcalculated length at first annulus formation	79.7	73.8-85.6	8
Length of one year olds in June 1980	101.2	97.7-104.6	8

* where 0.16 = regression intercept of otolith size at formation
Other codings as in Table 19.

Figure 25. Growth of P. laeta inferred from lengths of 1980 fish. Solid circles mark mean value, vertical bars 95% confidence intervals. Squares note backcalculated lengths at the end of a year's growth ± 95% confidence intervals based on otolith analysis. Sample sizes noted near plots.

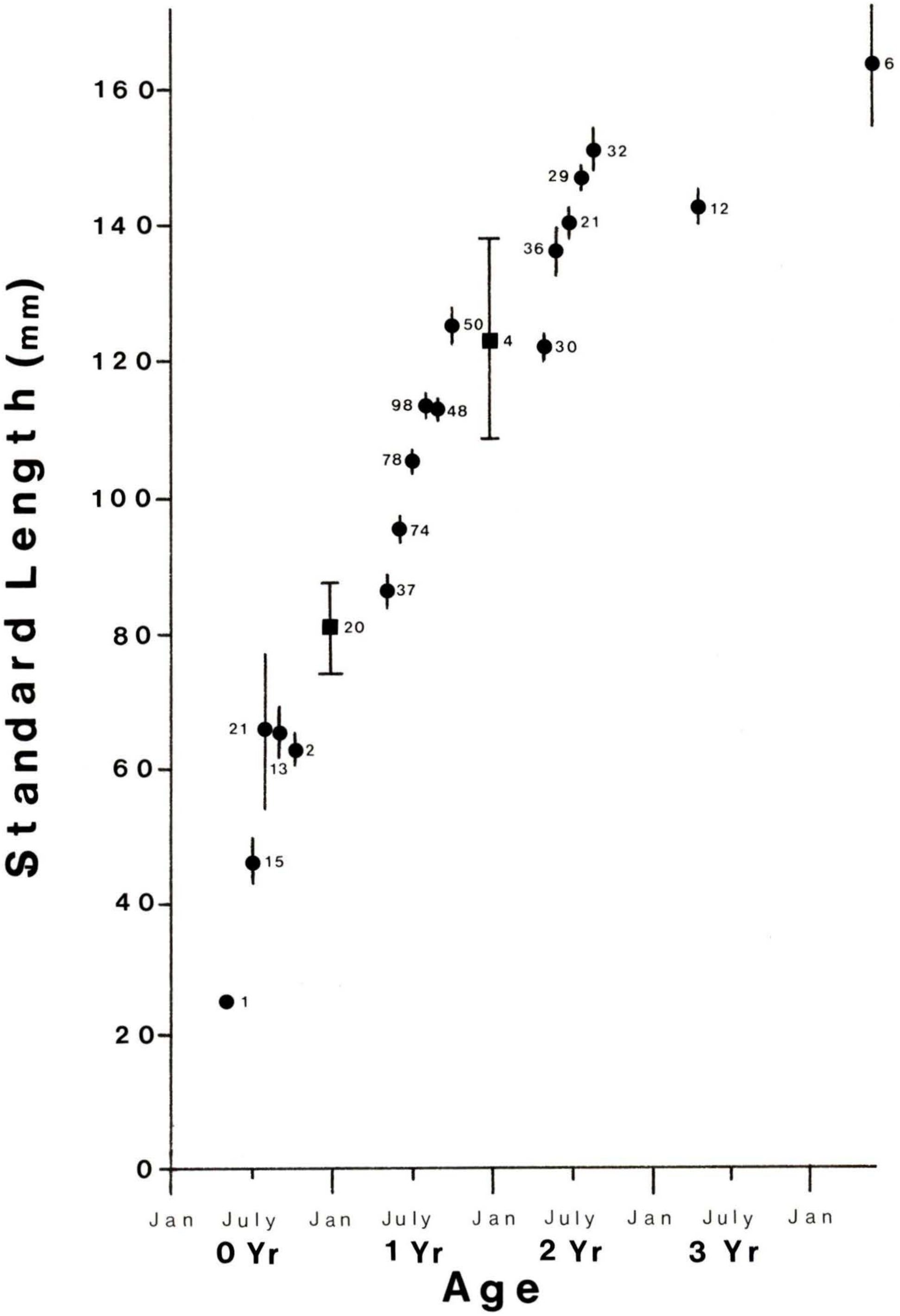

Standard Length (mm)
160
140
120
100
80
60
40
20
0
Jan
July
Jan
July
Jan
July
Jan
July
Jan
0 Yr
1 Yr
2 Yr
3 Yr
Age
1
15
21
13
2
20
37
74
78
98
48
50
4
30
36
21
29
32
12
6

Figure 26. Growth of P. ornata inferred from lengths of 1980 fish. Codings as for Figure 25.

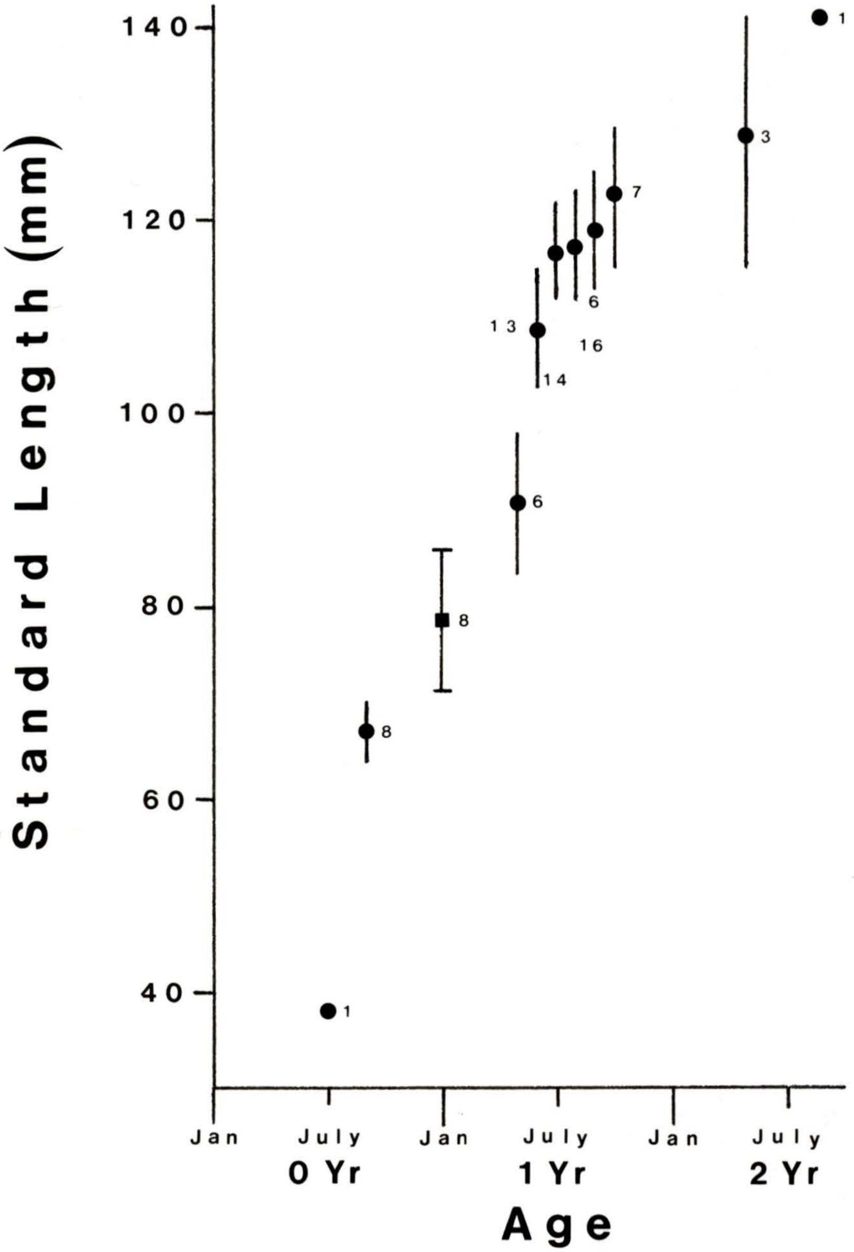

Standard Length (mm)
140
120
100
80
60
40
1
8
8
6
13
14
16
6
7
3
1
Jan
July
Jan
July
Jan
July
0 Yr
1 Yr
2 Yr
Age

TABLE 21

AGE GROUPINGS WHERE PHOLIS SIZES ARE NOT SIGNIFICANTLY DIFFERENT

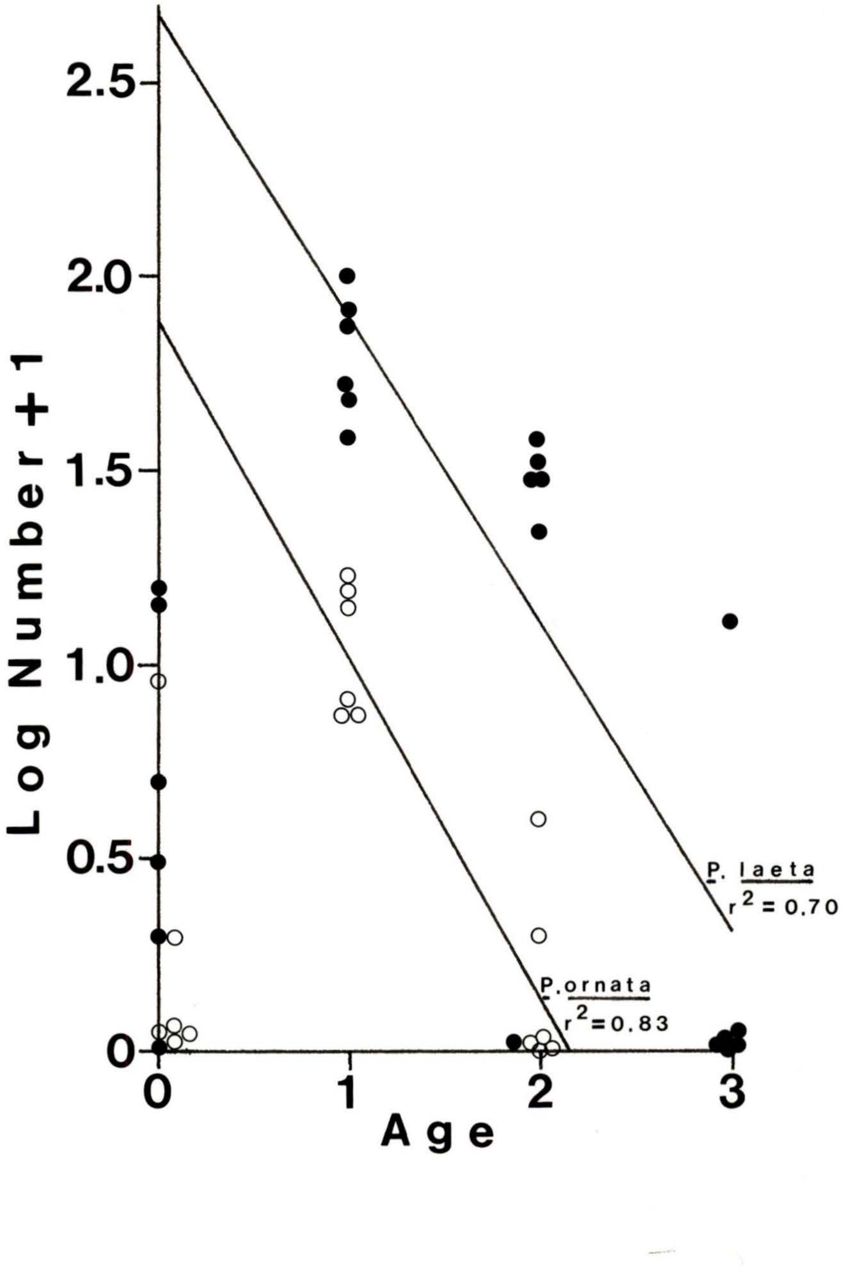
P. laeta - overlapping size ranges shown on one line

May 0 years
July 0 years
Aug., Sept., Oct. 0 years
May 1 year
June 1 year
July 1 year
Aug. Sept. 1 year
Oct. 1 year, May 2 years
June 2 years, July 2 years, May 3 years
Aug. 2 years. May 3 years
Aug. Sept. 2 years
May 4 years

P. ornata - overlapping size ranges shown on one line

July 0 years
Aug. 0 years
Sept. 0 years
June, July, Aug., Sept. 1 year
July, Aug., Sept., Oct 1 year, May Sept. 2 years

Figure 27. Catch curves of _P. laeta_ (solid circles) and _P. ornata_ (hollow circles) with fitted mortality curves based on abundances of fish of one year or older. Calculated from 6 months of eelgrass sampling during 1980.


Log Number + 1
2.5
2.0
1.5
1.0
0.5
0
0
1
2
3
Age
P. laeta
$r^2 = 0.70$
P. ornata
$r^2 = 0.83$

P. ornata were less abundant than *P. laeta* and the *P. laeta* to *P. ornata* ratios increased with age. This is intuitively obvious from the lack of *P. ornata* of sizes equal to the largest *P. laeta*, and probably reflects the higher mortality of *P. ornata*.

Reproduction of P. laeta

Habitat

Mature *P. laeta* and juveniles were abundant in the intertidal and shallow subtidal rocky areas of Patricia Bay during the winter months of 1979-80, 1980-81, 1981-82. In the area examined there were no interspaces between the rocks and the substrate so *P. laeta* must be able to force themselves, or dig their way, underneath the rocks. The most common case had only one mature male and one mature female under a rock unless the rock was large (greater than 0.3 m diameter or so)(Table 22), when sometimes 2 breeding pairs were found.

P. laeta at the end of their first year were immature with egg size averaging 0.14 ± 0.01 mm SE (N = 40). (See coding for January captures, Figure 23).

Breeding Colouration

Mature males develop an orange or reddish colouration along the cheeks, throat, pectoral fins and ventral region anterior to the vent. In females, these areas are typically creamy or faint green coloured year round.

TABLE 22

THE OCCURRENCE OF P. LAETA UNDER ROCKS SHOWING THE HIGH RELATIVE FREQUENCY OF ONE BREEDING PAIR PER ROCK

Number of *P. laeta* present			Frequency
Mature male	Mature Female	Immature	
1	1	0	21
2	2	1	1
1	1	1	2
1	1	2	2
0	1	0	1
1	0	2	1
0	0	1	1

Timing of Reproduction

No egg masses were located when sampling on December 9, 1980 or January 9, 1982. However, egg masses were present January 17, 1980, January 29, 1980 and February 14, 1980. Therefore mid-January seems to mark the beginning of egg laying. Of 7 egg masses found in 1980, 4 had 2 adults coiled around the egg mass, and 3 had one adult.

No egg masses were found April 18, 1980 when the tides were next sufficiently low to allow observation (0.6 m) and presumably hatching had occurred.

Egg diameter, as an index of time of spawning, shows a marked reduction between sampling on January 17, 1980 and February 29, 1980 (Figure 28).

Fecundity

Large, presumably mature eggs were only found in *P. laeta* over 100 mm SL. Fecundity increases with length up to approximately 1600 eggs in females 134 mm SL (Figure 29). Only one ovary was found in any of the specimens examined.

Laboratory Spawning

Five pairs of *P. laeta* captured from Patricia Bay December 9, 1980 spawned in the laboratory. Spawning was not observed but egg masses were first evident on January 19 (2 egg masses), January 20 (2 egg masses), and January 23 (1 egg mass), 1981. Eggs are white in colour and adhere to themselves, but not to the cover above or

Figure 28. Diameter of eggs from P. *laeta* showing reduction indicating spawning of large eggs between Jan 17 (solid circle) and Feb 29 (open circles). Each point is the mean value of 10 largest eggs per female, vertical bars are 95% confidence intervals.

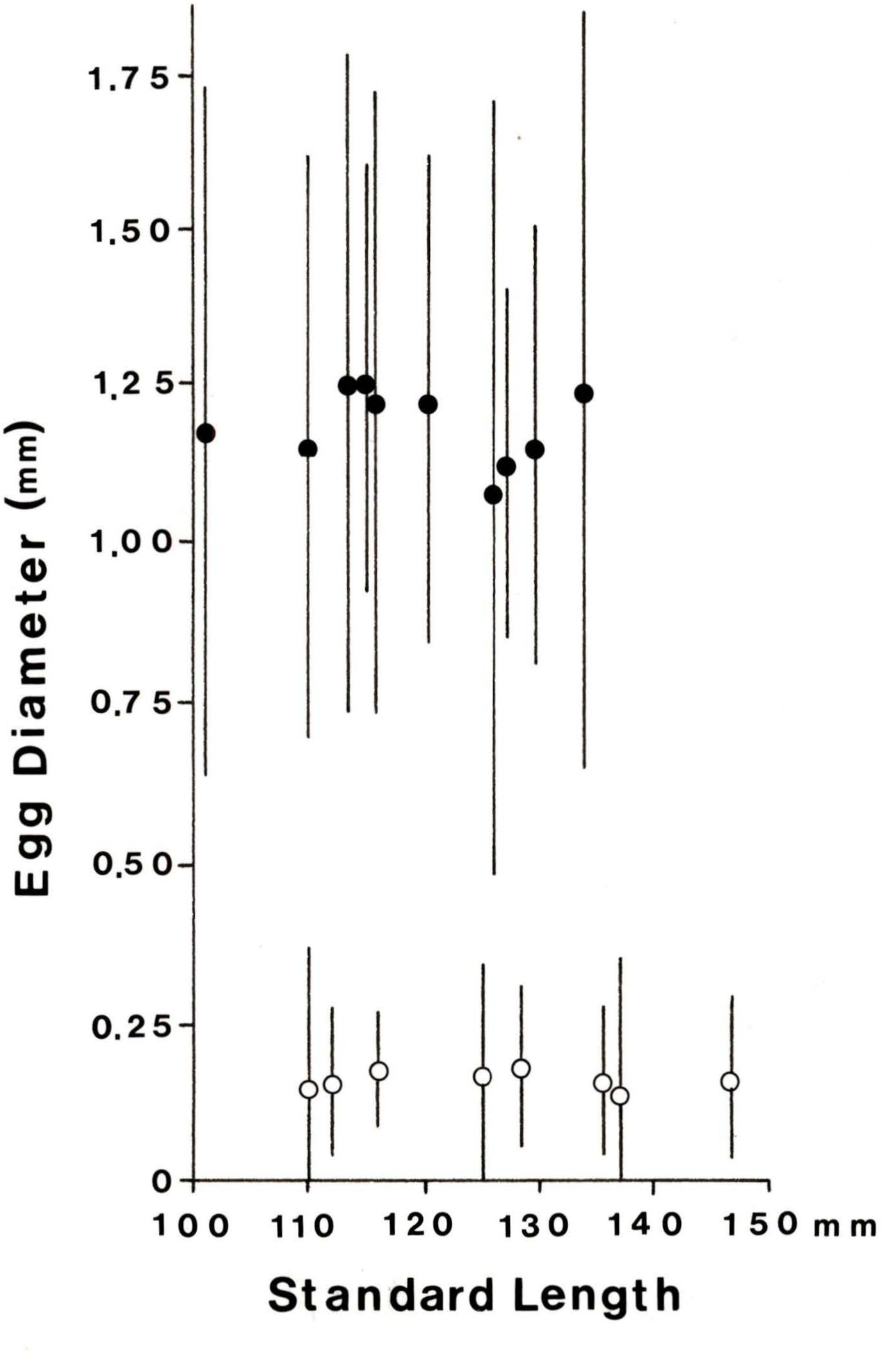
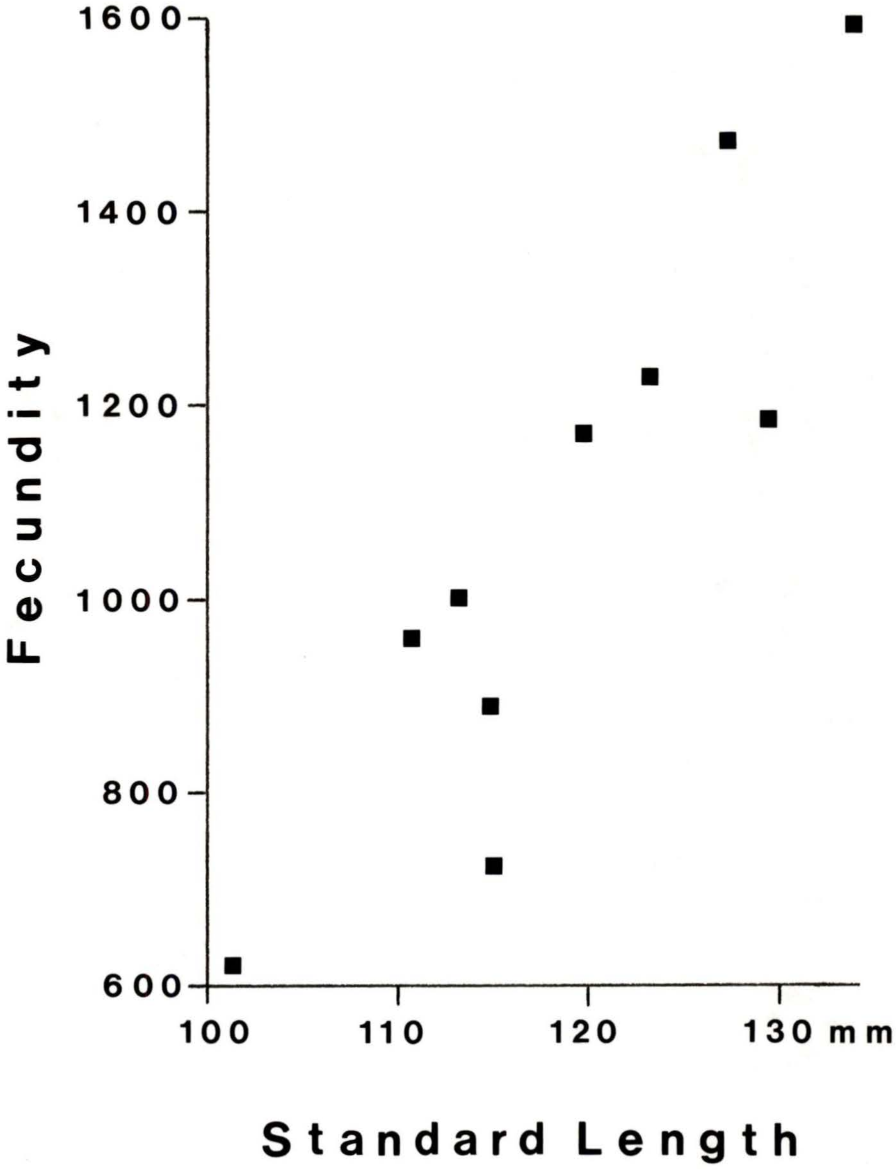

1.75
1.50
1.25
1.00
0.75
0.50
0.25
0
Egg Diameter (mm)
100
110
120
130
140
150 mm
Standard Length

Figure 29. Graph of egg number against *P. laeta* size showing increased fecundity with growth. All eggs contained in the ovaries were enumerated.


1600
1400
1200
1000
800
600
Fecundity
100
110
120
130 mm
Standard Length

the substrate below. Daily observations suggest that while *P. laeta* do coil around the egg mass at times, this guarding is not necessarily consistent (Table 23). As egg development proceeded the eggs became a creamy colour and the egg masses tended to break into clumps. Eggs hatched from 3 egg masses from March 20-23. Eggs in one tank disappeared and may have been eaten. The egg mass in the 5th tank did not hatch. Larvae were positively phototactic after hatching and showed some growth (Figure 30), but could not be induced to feed and subsequently died.

Reproduction of P. ornata

No spawning pairs of *P. ornata* were located during this study despite additional efforts to trawl or trap specimens to a depth of 60 m during the winter months. However, analysis of egg size throughout the summer (Figure 31) shows that young of the year do not mature but one year olds do. Only one ovary was found in the females examined. Males have two tightly joined testes and all (N = 19) one year old males caught during September had a small but noticeable genital papilla which is not developed in female *P. ornata* of similar size. *P. ornata* do not breed during their summer residency in the eelgrass so I presume breeding occurs during the winter months in unknown habitats.

TABLE 23

SUMMARY OF LABORATORY OBSERVATIONS OF EGG GUARDING IN 5 *P. LAETA* PAIRS

Number of observations	83
Female only guarding	4
One adult guarding	15
Male and female guarding	8
No guarding	56

Figure 30. Sizes of P. *laeta* larvae showing some growth for 24 days after hatching plotted as mean (solid squares) and 95% confidence intervals (vertical line) based on 3 larvae per day.

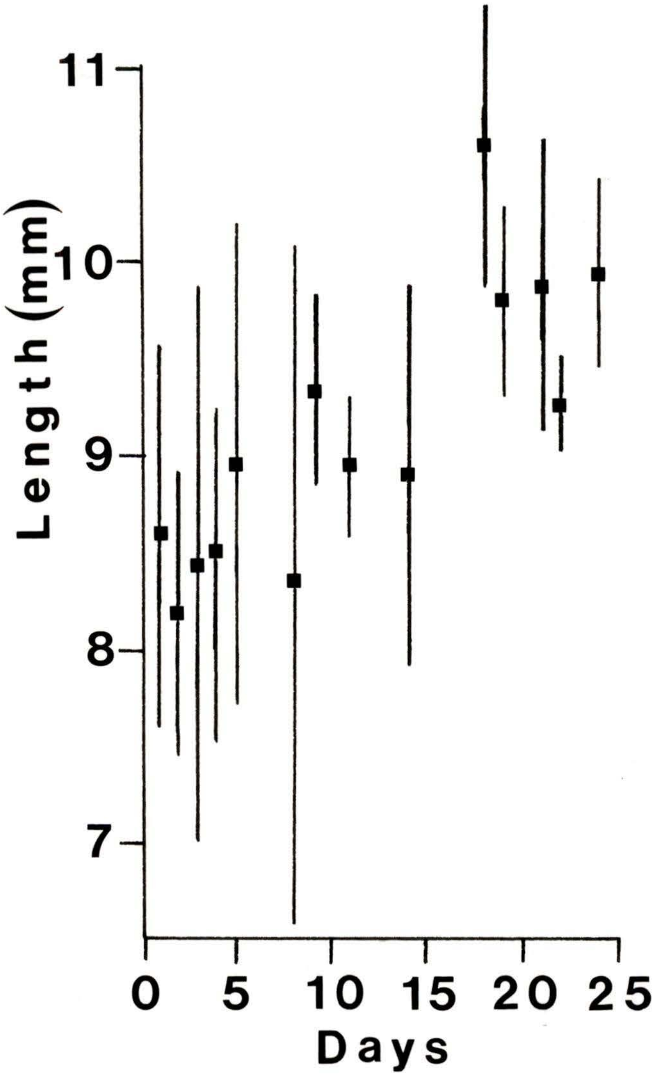
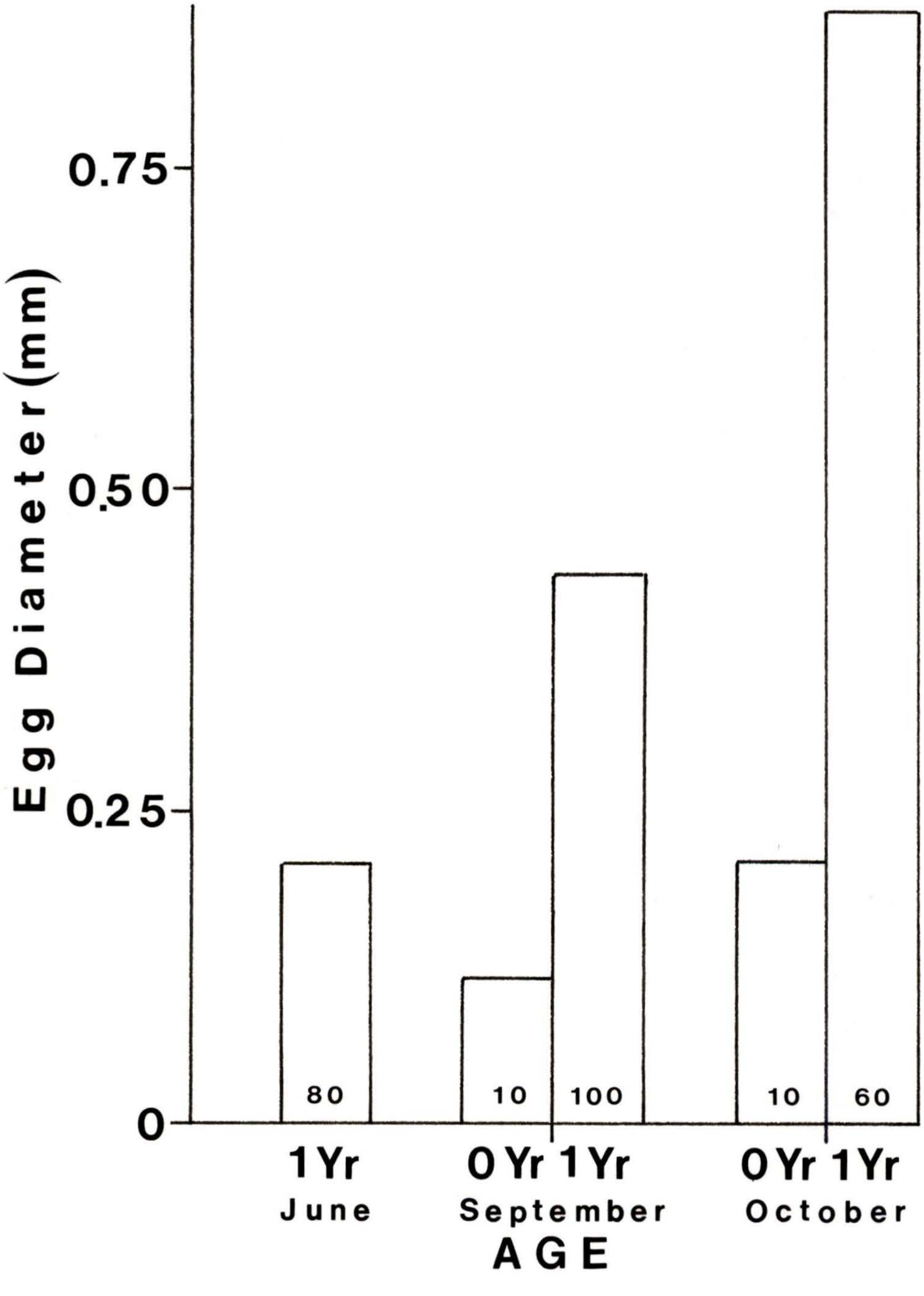

Length (mm)
11
10
9
8
7
0
5
10
15
20
25
Days

Figure 31. Egg diameter of _P. ornata_ at 3 different times during the year showing that one year old fish mature (N = 24) but young of the year do not (N = 2). Number of eggs measured noted in histograms.


Egg Diameter (mm)
0.75
0.50
0.25
0
80
10
100
10
60
1 Yr
June
0 Yr 1 Yr
September
0 Yr 1 Yr
October
AGE

Discussion

Aspects of Niche Theory

Discussion of the particulars of this study requires consideration of the reasons for assuming that the parameters measured are useful quantifiers of the ecological relationship between these two syntopic pholidids. According to Levins (1968), the number of niche dimensions, plus measures of niche breadth, niche overlap and community diversity are the parameters sufficient for the study of niches and community structure. Measures of community structure were not attempted in this study except for recording the presence of other fish species. Therefore only the first three aspects have been considered here.

Niche Dimensions

Niche dimensions refer to the number of factors that serve to separate species (Levins 1968) and are generally of three basic types: spatial, trophic or temporal (Pianka 1973). These three niche dimensions commonly investigated account for all subdivisions of four dimensional space plus food niche measures. Habitat use differences between species are generally more important than food differences which are important more often than temporal differences based on many ecological studies summarized by Schoener(1974). As the chance of two identifiable species being identical is low it seems likely that a sufficiently precise and detailed search would result in the detection of some differences between species (Schoener 1974). It is therefore the magnitude and ecological importance of the differences found that are of primary importance in the understanding of interspecific relationships, not merely the fact that differences exist.

Niche Breadth/Niche Width

Niche breadth, or niche width is a measure of the diversity or variability of the use of one particular niche dimension as determined by functions involving both the range and evenness of resource use. Because of this, the measures of niche breadth such as those of Levins (1968) and Pielou (1972) are affected by the degree of subdivision of niche dimensions considered, in addition to the frequency of occurrence of the number of the various subdivisions. Increasingly subdividing variables that can only be treated as discontinuous variables increasingly widens the calculated niche breadths. The units may be the number of subdivisions of habitat, food types, or groupings of time intervals when considering breadth of habitat utilization, food utilization or activity patterns respectively. Hespenheide (1975) has also emphasized for food utilization in birds, that a biologically realistic value of niche width requires that animals make similar or identical distinctions or lack of distinctions with respect to prey type. Soulé and Stewart (1970) also suggest that it is highly anthropocentric to speak of the width of niches. They consider the possibility in birds of a "wider niche" when birds feed on plant and animal and a "narrower niche" when feeding on seeds and berries whereas from the point of view of a bird a caterpillar and a berry may be more similar than a seed and a berry.

I compared the niche breadth of _P. laeta_ and _P. ornata_ as measures of diversity of the use of the resources, although this procedure may have equally weighted niche dimension subdivisions perceived to be radically different by the fish. Both species are assumed to make identical distinctions between subdivisions of habitat, food or time of day. The niche width measures can then be used to relate to aspects of specialization (low diversity) or lack thereof (high diversity) of the species' ecologies.

Levins' (1968) niche breadth measure assumes equal availability of resources. However, I considered it to be beyond the scope of this investigation to determine the availability of each prey type for analysis of food utilization especially as one should determine if all potential food items censused were actually available to _P. laeta_ and _P. ornata_. This would be impossible to determine without extensive testing and I have therefore assumed equal availability. However, as Fensinger and Spears (1981) have noted, if resources are not equally available, the species whose members as a group tend to use resources in proportion to their availability can be considered to have a broader niche than those that do not. Therefore, deviations from this assumption would affect the measures of niche breadth, if considered as the proportion of similarity to the resource base.

Niche Overlap

Niche overlap in ecological communities is defined as the joint use of resources by coexisting species (Harner and Whitmore

1977). Pianka's (1973) calculation of overlap used in this study has the advantage of a ready geometrical interpretation, is symmetrical, can not exceed 1, and measures the pattern of resource use and is therefore insensitive to the absolute number of the two species using the resource (Slobodchikoff and Schultz 1980). When niches are separated along any single niche dimension then both niche overlap along that dimension and overall niche overlap are 0 (Pianka 1973). In addition, when the utilization functions on the various resource dimensions are independent, then the total overlap of the two is equal to the product of the overlaps (May 1975). However, in this study it is unlikely that the dimensions of habitat use, food type, food size or activity patterns are orthogonal so bivariate functions were not calculated.

As noted by Schoener (1968) there is a subjective component to the calculation of niche overlaps. If the subdivisions are too gross then the entire frequency distribution of both species may be incorporated into one category (e.g. if only two habitat zones - greater or less than 100 m depth were used - a complete overlap of _P. laeta_ and _P. ornata_ habitat utilization would result). Coarse subdivisions therefore result in overestimation of overlap. Minute subdivisions usually result in smaller overlap of resources but possibly not entirely due to the species' abilities to distinguish and choose between various subdivisions of that dimension (prey type for example). Food choice may be confounded by microhabitat or temporal differences between predators and overlaps in food utilization in the absence of these confounding factors may actually be higher than recorded.

There are no simple statistical methods for calculating confidence intervals for comparing 2 or more overlap indices, although in a typical study using N = 25 (similar to my samples for stomach contents) one can expect a standard deviation of 0.05 to 0.10 at overlap of 0.50 (Ricklefs and Lau 1980). From this, differences of 0.10 to 0.20 could be used to reject the null hypothesis that the two indices were drawn from the same sampling distribution (Ricklefs and Lau 1980).

Niche overlap indices have often been adopted as measures of competition and have also been employed in community analyses, and used as predictors of species coexistence or lack thereof (Hurlbert 1978). However, extensive niche overlaps may represent either the presence of competition in the past, or present, or may actually be correlated with reduced competition (Colwell and Futuyma 1971, Pianka 1974, Hurlbert 1978, Slobodchikoff and Schultz 1980). To resolve this dilemma one must investigate overdispersion of niches (Schoener 1974), actual versus virtual niche overlap (Colwell and Futuyma 1971), use perturbation experiments (Schroeder and Rosenzweig 1975), test for the effect of changing of population densities on resource use or fitness (May 1975), or else document that resources in common to the ecology of both species are limiting (Hurlbert 1978). These types of extensive investigations were beyond the scope of this study and others dealing with inshore fishes such as Miller _et al._ (1980), so I restrict the interpretation of overlap measures to similarity of resource use but draw no inferences regarding competition.

Overall Relationship of Niche Parameters

The dimensions selected were artificially subdivided to an extent likely to show reduced overlap along the dimensions. I hoped to avoid increasing the measure of niche breadth artificially by subdividing a dimension to an extent larger than considered to be perceived by *P. laeta* or *P. ornata*. Comparison of the values of niche breadth and overlap calculated in this study with other species are valid if the dimensions are divided to a similar extent assuming all species considered can make similar distinctions between dimension subdivisions. These restrictions and a lack of standardization of methods when researching fish ecology make comparisons with other published fish studies difficult.

Habitat Utilization

Seasonality

Both *P. laeta* and *P. ornata* show marked seasonality in the use of the eelgrass beds which is probably due either to innate cues or else responses to changes in environmental conditions. Retreat from the *Zostera* was not due to a lack of cover as *Zostera* occurs year round although some dying off occurs during the winter months. Lack of food should not be a problem in the autumn months as many of the commonly taken prey items occur year round, e.g. *Macoma* sp., *Caprella laeviscula* (Caine 1980), *Anisogammarus pugettensis* (Chang and Parsons 1975). Based on Herlinveaux (1962) the surface water temperature and salinity conditions in Saanich Inlet from October to November change from 13°C to 6°C and 29°/oo to 25°/oo respectively when averaged for the years 1931-1960. The winter 1980-81 dilution resulted from runoff of early winter rains and resulted in a larger than normal salinity drop compared with Herlinveaux. However, as his data come from an oceanographic station in the centre of Saanich Inlet midway between Mill Bay and Patricia Bay it seems likely that his recorded salinity drop would be less extreme than the beach seine areas closer to runoff sources. It is possible that other factors besides salinity changes may have caused *Pholis* to leave the eelgrass between October and November such as changes in water temperature, changing day length, or intrinsic factors such as a stimulus to search for breeding habitat. It is apparently an annual phenomenon based on 3 winters of observation (1978-79 preliminary fieldwork plus 1979-80 and 1980-81) in Saanich Inlet. Additionally, D. Wilkie (personal communication) notes from his work in Burrard Inlet that few *Pholis* were found in eelgrass during the winter, but were instead located under rocks intertidally. *P. ornata* are present in eelgrass beds in the summer but not in the winter in Yaquina Bay, Oregon (Barton 1982).

Winter

In Saanich Inlet, *P. laeta* breed in the intertidal and shallow subtidal zone and presumably *P. ornata* breed at greater depths. In Alaska, *P. laeta* are absent from eelgrass in the winter presumably to avoid freezing in the shallow waters and apparently move offshore (Smith and Paulson 1977) as they are not found intertidally. *Pholis gunnellus* breed offshore in the western Atlantic where their movement from the shallows is in response to temperature change (Burgess 1978), although some breed intertidally in Wales (Sawyer 1967) where freezing is not a problem. *P. ornata* retreat from the eelgrass during the winter months in Yaquina Bay, Oregon, whereupon they inhabit the estuarine intertidal zone under rocks (Barton 1982). They do not interact with *P. laeta* which have a distribution restricted to more exposed areas (see Barton 1982) possibly due to *P. laeta*'s intolerance of warm summer water temperatures in Oregon estuaries.

The general habitat utilization where either or both *P. laeta* and *P. ornata* occupy *Zostera* beds therefore involves the species leaving the beds in the winter, although considerable variability in habitat of winter residency exists between species and localities.

In areas just south of British Columbia bordering on the exposed coast (e.g. Grays Harbour, Washington; Tillamook Bay, Oregon), *P. ornata* are found in estuarine intertidal habitats under rocks during the winter in the absence of *P. laeta*, and in one case (Port San Juan, B.C.) I have found 18 *P. ornata* with 2 *P. laeta* under rocks in the San Juan River estuary during the spring of 1980. Therefore there may be an interaction between the more common *P. laeta* and *P. ornata* where they coexist in Saanich Inlet with the resulting displacement of P. ornata to deeper water. It is also possible that the species have different environmental preferences when occurring in estuarine conditions near exposed coasts compared with less saline winter conditions in protected

waters. In any event, the winter separation in Saanich Inlet results in a premating isolating mechanism, and none of the more than 1000 specimens examined appeared to be hybrids.

Summer

Although both Pholis species coexist in the eelgrass during the summer they differ in their microhabitat usage. The simplest explanation for P. laeta's distribution is that the species is closely associated with the Zostera without obvious depth preferences but does not venture into the intertidal zone to a large degree. Marked fish recovery data support the conclusion that there are no depth preferences and further suggest that the fish do not move around much based on the recovery of specimens from the same 10 m wide transect at least 1 month after marking. Caprellids, upon which P. laeta feed heavily, are usually found on eelgrass blades (Caine 1979, Kozloff 1973) but not on the intertidal mudflat. This is correlated with the P. laeta distribution.

The distribution of P. ornata subtidally and intertidally could be due to a number of reasons such as a preference for warmer (shallower) water or an innate searching pattern in the intertidal zone. The most parsimonious explanation however, which I can not disprove is that P. ornata is distributed randomly at high tide without regard for the eelgrass boundary and is therefore more likely than *P. laeta* to be found intertidally at high tide, and in the shallowest water at low tide when the fish retreat to prevent emersion. Unfortunately, for logistical reasons I have no data on the abundance of *P. ornata* in the lower eelgrass bed at high tide to test this explanation.

Niche overlap measures for subtidal use by *P. laeta* and *P. ornata* are quite high, but similar to values reported for overlaps between *Clinocottus analis*, *Oligocottus snyderi* and *Artedius lateralis* in the intertidal zone of California (Yoshiyama 1980). However, when the tides are not low in Saanich Inlet, niche overlap would be 36% lower due to the disproportionately high number of *P. ornata* on the mudflat (i.e. the overlap between high tide use and low tide use is 0.64).

Calculated niche breadths show that *P. ornata* has a narrower niche than *P. laeta* when only the subtidal captures are considered. However, the *P. ornata* niche breadth at high tide could be larger than at low tide assuming that not all *P. ornata* in the eelgrass entered the intertidal zone. Overall, it is impossible to ascertain whether *P. laeta* is more specialized by staying in the *Zostera*, or if *P. ornata* is by exploiting the intertidal zone without subtidal *P. ornata* densities determined at high tide.

The analysis of variance of depths used excluded the May and September values for fish density when migration was assumed to be a factor. It is possible that the peak density in the deeper water at Mill Bay during May was due to both species returning from breeding habitats but not yet ranging throughout all eelgrass depths. Little intertidal breeding habitat is located immediately next to the Mill Bay beach seine location so P. laeta may have been in shallow subtidal depths similar to the 5 m depth from which P. laeta were captured from Patricia Bay (Table 7). Presumably P. ornata returned from even greater depths. The October data do not show a similar deep peak of abundance possibly because emigration from the eelgrass had not yet commenced.

Eelgrass use by both Pholis species shows that some young of the year occur in the canopy. Marliave (1977) has shown that P. laeta larvae preferentially settle on Phylospadix (and presumably Zostera in protected coastal regions where Phylospadix does not occur) where they entwine themselves around the blades. Both species presumably settled out from the plankton in spring or early summer and remained in the canopy at least until July when sampling was conducted. As no Pholis were captured by nightlighting at Patricia Bay in late April and early May 1980 at Patricia Bay, nor by Barraclough et al.(1968) in a fine mesh surface trawl from April 23 to July 21, 1968, presumably the settling occurs before late April. Barton (1982) notes settling of P. ornata larvae in the intertidal rocky area of Yaquina Bay as early as March, but no juvenile P. ornata or P. laeta were observed by me in the rocky intertidal zone of Patricia Bay.

As adult P. laeta and P. ornata were not captured in large numbers from the canopy, but were easily caught by the same netting method from near the bottom, perhaps there is a change in behaviour as the fish grow larger and leave the canopy. A change may be partially due to the increase in weight of the fishes with growth and a resulting reduction in support by the eelgrass. It is also possible that larger fish, if they occurred in the canopy, may have been able to avoid the net to a greater degree than either the young in the canopy or the fish along the bottom but this was not determinable.

Food Utilization

Prey Taxa

Prey types taken by small *P. laeta* and *P. ornata* are similar and consist mainly of harpacticoid copepods which live on *Zostera* as well as in close contact with the substrate (Kozloff 1973, Kask *et al*. 1983). These prey are presumably available to those fish that occur in the canopy as well as those on the substrate although the exact use of the two microhabitats by the young has not been determined. Young of both species have similar numbers of teeth, (Peden and Hughes 1982 ms) and similar jaw length, so there is no reason to expect different prey utilization based on these characters. Smallest *P. ornata*, however, did have small amounts of other prey (eggs and polychaetes) which were absent from *P. laeta*.

Harpacticoid copepods have been found to make up 10.2% of the IRI of *P. laeta* and 5.6% of the IRI of *P. ornata* from Puget Sound (Simenstad *et al*. 1979) and 51.04% of the IRI of *P. laeta* in the Strait of Juan de Fuca (Miller *et al*. 1980), although the sizes of fish examined were not noted. These prey therefore make up part of the diet outside Saanich Inlet as well.

Larger *Pholis* of both species show a dietary shift in food type. The primary prey of *P. laeta* greater than 100 mm (SL) is *Caprella laeviscula*, a species that occurs on *Zostera* blades where it holds on with hind legs (Kozloff 1973). Populations of *C. laeviscula* are dense in Puget Sound (Caine 1979) where they occur year round at a normal density of 177 per turion, with over 92% of the caprellids distally more than 50% along the turion from the substrate (Caine 1980). Presumably the case is similar in Saanich Inlet. In Puget Sound, caprellids occurred in over 50% of *P. laeta* examined by Caine (1979) but in small amounts (3.5% of the diet). Caprellids were not mentioned as prey items of *P. laeta* or *P. ornata* by Simenstad *et al.* (1979) or Cross *et al.* (1978), based on fish from the same region. Miller *et al.* (1980) report that in the Juan de Fuca Strait caprellids were known from a sample of 49 specimens collected in 1978 but were not the dominant prey items (harpacticoids were), although the size of the specimens examined in the above studies were not reported. Variability therefore, could be due to a combination of differences in location, and mixtures of fish of different sizes in the different studies referenced here. Additionally, Simenstad *et al.* (1979) show that gammarid amphipods accounted for 78.4% of IRI of *P. laeta* from Puget Sound and 85.4% of IRI from the San Juan Islands, but as their beach seines were not restricted to eelgrass beds, perhaps these differences from the *Caprella* dominated samples of my eelgrass collected *Pholis* are not surprising.

Other prey of less importance to larger *P. laeta* from Saanich Inlet include gammarid amphipods, polychaetes and the hippolytid shrimp *Hippolyte clarki*. Shrimp of this species are green in colour and occur on *Zostera* where they orient lengthwise along the blades (Morris *et al*. 1980).

It is therefore apparent that the characteristic microhabitat of two of the prey items (*Caprella* and *Hippolyte*) is on the eelgrass blades themselves. Prey were usually found whole in the stomach.

P. ornata of larger size have larger proportions of *Macoma* siphons, *Leptochelia dubia* or *Anisogammarus pugettensis* than *P. laeta* or small *P. ornata*. These prey items are found primarily in or on the benthos. *M. nasuta*, specimens of which I dug up from the intertidal zone at Patricia Bay and Mill Bay, are commonly found in the substrate of eelgrass beds but decrease in abundance with depth (Shelford 1935). The species has separate inhalant and exhalant siphons (as do all *Macoma* (Quayle 1960)), orange in colour and feed by either suspension feeding (Reid and Reid 1969) or deposit feeding (Hylleberg and Gallucci 1975). In either case, protruding siphons are presumably nipped off by *P. ornata* and apparently little sand is ingested as virtually none was found in stomachs upon dissection. This nipping off of siphons constrasts with the feeding ecology of large *P. laeta* which usually take prey whole and may be facilitated by the greater number of jaw teeth in large fish (twice as many as *P. laeta*, Peden and Hughes 1982 ms.)

Few siphons were noted in *P. laeta* stomachs, perhaps due to *P. laeta*'s disposition to feed on caprellids in the canopy, their possible inability to bite off siphons efficiently, or both. As few caprellids or hippolytid shrimp were noted from *P. ornata* stomachs, there is a marked difference in the feeding ecologies of these two species with respect to prey location as well. This correlates with the observed microhabitat partitioning of the intertidal zone at high tide as, in addition to intertidal *Macoma*'s, *Anisogammarus pugettensis* occur intertidally year round at Crescent Beach, Georgia Strait (Chang and Parsons 1975) and hence presumably in the same habitats in Saanich Inlet. A number were found under the rocks used to weight the lead lines of the intertidal traps set in June 1981 at Patricia Bay.

In addition to *Macoma* and *Anisogammarus*, a third important food item, *Leptocheilus*, more common to *P. ornata* than *P. laeta*, are known from lower intertidal eelgrass beds (Levings and Rafi 1978) where they live in the sediment (Kozloff 1973).

These food habits of *P. ornata* differ somewhat from the report of Simenstad *et al* (1979) in the Puget Sound area where 49.7% of IRI were gammarid amphipods and 32.9% were oniscoidean isopods (*not* found in *P. laeta* stomachs examined by them). There is therefore a difference in food taken by *P. ornata* even between nearby geographic areas, just as was noted for *P. laeta*. However, the presence of large numbers of oniscoidean isopods in *P. ornata* but not *P. laeta* may be independent evidence for the species differentially using the intertidal zone at high tide. Oniscoidean isopods, as a group, primarily occur in the upper intertidal or terrestrial habitats and are adapted to prolonged emersion (Green 1961, McLaughlin 1980). At least 3 species are known from moist sand under debris in the upper tidal zone in Washington and adjoining areas (Hatch 1947). Perhaps their occurrence in *P. ornata* but not *P. laeta* is due to *P. ornata*'s greater likelihood of occurring high in the intertidal zone.

Other authors have provided further information on the diet of *P. ornata*. Miller *et al.* (1980) note a high occurrence of bivalves based on 3 fish from the Juan de Fuca Strait captured during 1978. Caine (1979) reports that few *P. ornata* take *Caprella* (1 out of 14 for 5.9% of total diet), but provided no additional data on *P. ornata* diets. Barton (personal communication) reports that *P. ornata* in Yaquina Bay, Oregon, feed upon clam siphons. In California *P. ornata* take small crustaceans and shelled molluscs (Fitch and Lavenberg 1975). Therefore considerable variability exists. The common denominator of prey taken by large *P. ornata* is benthic location. As a number of young *P. ornata* occur in the canopy, there must be a behavioural change to accommodate this shift. In comparison, young *P. laeta* feed in the canopy so the source of food for *P. laeta* does not change as much as they grow although the *Zostera* blades may not fully support the adult *P. laeta* that feed in them.

Concordance

Kendall's measure of concordance quantifies whether or not the overall rankings of the proportions of prey types between individual fish of a size grouping are correlated and, if so, enables the best estimate of the true ranking of the prey importance by summation of the ranks assigned to each prey type for each fish in a size class (Siegel 1956). I believe this to be a useful measure of how representative the order of food importance is as the record of the diet. It provides a measure of the importance of various prey types that is independent of the number of prey items involved (which may be of radically different sizes and hence of different importance), and eliminates the large effects that an infrequently occurring item of large size would have if prey importance was based solely on the total EA of each prey type in a fish size group. Lack of concordance shows that significant variability exists between the diets of the individual fish in a grouping.

All but one *P. laeta* size group exhibit concordance. The nonconcordant group was of intermediate size and represents a mixture of fish that were feeding on different prey types. This size group (80-100 mm) is at a transition between those sizes feeding mainly (and concordantly) on copepods (20-80 mm) and those feeding on caprellids (100-180 mm). Perhaps *Caprella* are somewhat too large, and copepods inefficiently small for *P. laeta* of 80-100 mm on average. Or, coupled with this, a learning component involved in the prey type switch at this time could be the explanation of the differential use of prey by members of this size class.

P. ornata showed concordance only 50% of the time. Small sized fish that fed with greatest frequency on copepods had other primary prey (eggs and polychaetes) in a sufficiently large number of fish to prevent concordance. Additionally, *Anisogammarus* were the most frequently occurring prey in the largest *P. ornata* size class but concordance did not exist. Only the 3 intermediate size groupings of *P. ornata* (60-120 mm SL) took prey in a consistent order of importance. Coincidentally, these 3 groups were those in which siphons occurred as the primary prey item.

Overall, there is more individual variability in the prey taken by *P. ornata* than by *P. laeta*. This adds uncertainty to the correlation and overlap measures of prey taken by the two species, as they are based upon tabulations of the diets of whole size groups.

Diet Correlation

Nonparametric statistics such as rank correlation have been used to test for differences in diets between *Fundulus parvipinnis* and *F. heteroclitis*, *F. heteroclitis* and *F. diaphanus*, as well as for interpopulational differences in *F. heteroclitis* (Fritz 1974). That *P. laeta* and *P. ornata* show correlations between species at small sizes but not at large sizes, reflects their similar diet when small. The principal component groupings of the size classes show a decrease in the relatedness of three major classes - small *P. laeta* and small *P. ornata* being grouped into one class, large *P. laeta* as the second, and large *P. ornata* as the third.

Although axes can not be labelled in terms of one variable, factor 1 is likely to be heavily weighted with copepods, and factor 2 weighted with caprellids. Large *P. ornata*, which are low in the use of both copepods and caprellids, are resolved to a certain extent on factor 3 which may be heavily weighted in clam siphon frequency.

Diet Overlap

With a change in prey most commonly taken by both species with growth there is a reduction in food type overlap as the differences between fish size increase. The overall higher intraspecific overlap of *P. laeta* diets (0.441) is probably not significantly higher than the intraspecific *P. ornata* average overlap (0.291) assuming that a difference of 0.20 would be needed to reject the null hypothesis that the two indices were drawn from the same sampling distribution (Ricklefs and Lau 1980). Contrarily, the intraspecific *P. laeta* overlap is significantly higher than the interspecific overlap of these two species (0.226) although the average intraspecific overlap of *P. ornata* (0.291) is not.

These overlaps are much lower than the ≥0.82 for combinations of *Clinocottus analis*, *Oligocottus snyderi* and *Artedius lateralis* in California (Yoshiyama 1980). However, as his diet item groupings are much coarser than mine the results are not directly comparable.

The fact that the overlap of occurrence of prey types in the diet of either species is, on average, lower for *P. ornata*

($\Sigma v_j h_j = 0.165$) than for *P. laeta* ($\Sigma v_j h_j = 0.216$) is due to the greater number of resources and their distribution in the *P. ornata* diets.

P. laeta and *P. ornata* food utilization overlaps average much lower than the habitat overlaps. Although there are a different number of food and habitat dimension subdivisions it does not seem unreasonable to group the prey into 13 types because of the variety in the diet. From a purely ecological point of view, even if the taxa are subdivided more than can be recognized or grouped by *Pholis*, their overlap as a measure of diet similarity is likely to be an overestimation, considering that most groupings are to the family level and that unidentified material is included as one grouping. In fact, in terms of resource removal at the level of prey species, the overlap between *P. laeta* and *P. ornata* in the eelgrass is probably much lower than calculated here. This may be partially due to a reduction in habitat overlap as well and so the prey difference is due partially to fish taking what they may perceive to be different food, coupled with their differential habitat use (which affects the incidence of encountering food of the particular prey type which is to be selected). This differential encounter, times the differential use when encountered likely results in a lower measure of food overlap than would be measured if the two species did not differ in habitat use.

Because the prey types do not occur independently of the microhabitats examined it is impossible to compute a bivariate niche overlap measure as the product of the overlaps of habitat use and food use dimensions (May 1975). However, the food overlaps which I calculated already include food types specific to microhabitats as previously mentioned, so to that extent they are not completely independent of microhabitat use.

Diversity of Food Types

The niche breadth of *P. laeta* is narrower than *P. ornata* both when averaged for the size classes using Levins' (1968) formula (85% of niche breadth of *P. ornata*) and when calculated from Pielou (1972) (72% of niche breadth of *P. ornata*). The decrease in similarity of *P. laeta* to *P. ornata* niche breadth in the Pielou calculations results from the decreased weighting of the largest size class , in which *P.ornata* was less diverse than average. These calculations suggest that *Pholis laeta* is therefore a more specialized feeder.

There are few differences between the diversity trend to increase with growth when comparing prey by number and with prey measured as proportion of the diet. The increased diversity of *P. laeta* for 80-100 mm to 100-120 mm size classes, based on prey number of various types but not paralleled by an increase in diversity based on proportions, is due to a marked reduction in the number of copepods in the 100-120 mm size class and hence a reduction in the disproportionatey high weighting by number. This reasoning holds for the decrease in diversity of *P. ornata* diet, based on proportions of prey, between 40-60 mm and 60-80 mm which is opposite to the increase in diversity based upon number of prey of particular taxa. Overall increase in food type diversity with growth in both species is probably due to an increased number of taxa of manageable sizes for eating.

Pholis laeta and P. ornata niche breadth measures are similar to Keast (1978) for pumpkinseed (Lepomis gibbosus) based on 12 food categories using Levins' (1968) measure. Average diversity of prey (H) for P. laeta (0.38) and P. ornata (0.53) are generally lower than for O. snyderi (0.58), C. analis (0.98) and A. lateralis (0.43), Yoshiyama (1980) suggesting that Pholis laeta and P. ornata are more specialized feeders than these sculpins.

Food Size

As the mouth of fish species will affect the maximum size of food that can be taken it is not surprising that P. laeta and P. ornata do not differ markedly in the size of food they take. Jaw lengths are similar between fish of the same length. Pholis of 120-140 mm SL are the only interspecific equal sized combination to show a significant difference in food size taken. This is possibly due to a large quantity of Anisogammarus in P. ornata which were relatively large in size.

The increase in food size with growth is not unexpected (Hespenheide 1975) as it is presumably more efficient to take prey of near maximum usable size given equal handling time. Both species take prey of the same size throughout the first year of growth, but show a significant increase in prey size after 80 mm SL which coincides on average with the beginning of the second year.

P. ornata feed on similar sized prey throughout their second year before a switch in their 3rd year. P. laeta food size changes do not coincide with average sizes at the end of a year's growth except for at the end of the first year.

Overlap measures are very high based on 65 size groupings of EA (mm^2) primarily due to the extremely high frequency of prey in the smallest 3 groups for all but the largest P. laeta. The mean prey sizes of all but the largest P. laeta (140-180 mm SL) are smaller than prey taken by O. snyderi 41-70 mm SL, C. analis 35-145 mm SL and A. lateralis 41-110 mm SL (Yoshiyama 1980) which is probably not surprising given the markedly larger mouth sizes of the sculpins he studied, although fish with large mouths can still take small prey.

Heteroscedasity was due solely to the reduced variance of prey size in the smallest 3 P. laeta size classes. P. laeta at these size classes ate mostly copepods which varied little in EA. P. ornata of similar size took a wider variety of prey types and exhibited variation in prey size which was not significantly different than prey of the larger fish once converted to logarithms.

The niche breadth based on the proportions of different sized food averaged for each age group is higher for P. ornata than P. laeta which is due to a larger variance in the diet associated with a larger number and more even use of prey size groups. However, when the resource utilization of prey size is calculated the niche width of P. laeta is determined to be larger, because this technique also accounts for the distance between the groupings of these continuously distributed measures (Roughgarden 1974). Therefore, although there was a more even distribution of *P. ornata* food size in the mm^2 groupings the distances between *P. laeta* food size values were larger, resulting in a larger variance (see Table 16). As a species, *P. laeta* has the widest food size niche breadth although in many of the smaller size groups *P. ornata* is more variable in size of food taken.

The WPC and BPC of *P. laeta* and *P. ornata* are similar to *O. snyderi* (WPC 0.91, BPC 0.09) but quite different from *C. analis* (WPC 0.48, BPC 0.52) and *A. lateralis* (WPC 0.66, BPC 0.34) (Yoshiyama 1980). In addition, the shape of the *Pholis* resource utilization curves and *O. snyderi* (from Yoshiyama 1980) are similar with the largest proportion of prey taken being of the smallest size, and differ from *C. analis* and *A. lateralis* which show more even food size use. The high WPC of *Pholis* shows a large variation in the prey size use by an individual size class and the low BPC shows low variation between size classes in average resource use (Roughgarden 1974). Therefore, both *P. laeta* and *P. ornata* can be characterized as generalist users of a variety of prey sizes.

The WPC and BPC calculations are affected by the proportions of the different age classes present (or assumed to be present in the case of the young of the year). The very high WPC is due to a large variation in the prey sizes taken by the largest fish of both species. The increased weighting of age 0 fish, above what were actually captured, by logarithmic estimation of abundance results in a decrease of the WPC to the levels of 90% (P. laeta) and 90% (P. ornata) of niche breadth and are presumably closer to a minimum WPC expected than if raw catch data were used.

Activity Patterns

The presence of unevenly distributed activity patterns under constant dark conditions in both species strongly suggest that endogenous rhythms exist. The greatest amount of activity at the time of anticipated dawn under constant dark conditions, and a peak at dawn and dusk under photoperiod conditions, suggest that the species probably exhibit crepuscular activity (Hobson 1965) in the eelgrass beds. However, it is not always certain that activity patterns documented in the laboratory apply to field situations (Gibson, personal communication) as there is always the possibility that environmental variables which may fluctuate in the field, but which were constant in the laboratory, could affect the rhythms. For example, Gibson (1971) found that both light and water pressure affected the locomotory rhythm of Blennius pholis, a rocky intertidal fish from the northeastern Atlantic. An exogenous diurnal component affects the tidal rhythm of the species, as darkness has a suppressive effect on activity. Therefore both light and tide height can affect activity in some species but since tide height did not vary in the laboratory only indirect evidence for the effect of tides can be proposed.

I recorded activity from Pholis collected during the mornings in the month of July. Daybreak peaks in fish activity in the laboratory coincided with ebbing tides in the field. Evening peak activity (under photoperiod conditions) coincided with rising or high tides in Saanich Inlet and therefore correlation between the activity patterns shown in the laboratory with tidal cycles is not apparent.

Quantification of the food from the stomachs of both species collected on identical tide heights differing in time of day offers evidence that food gathering is not always related to tide height. Furthermore, low food totals in both species during the night suggest that the evening activity peak is not related to feeding, although the morning peak probably is.

The observed intertidal mudflat occurrences of P. ornata at high tide suggest that the lack of a tidal rhythm may be a liability. However, P. ornata are probably not at great risk of being emersed by receding tides in the intertidal mudflat because of the near uniform slope of the beaches. At a time that a fish perceived that the water was very low due to ebbing tides, it would still have a continuous pathway of water to escape through to greater depths. This is quite different from tidepool zones where tidal rhythms are well documented for fish species that occur there (Gibson 1967, 1971, Williams 1957). In these habitats fish may become stranded in pools of water as tides recede thereby becoming completely isolated from an escape route to the open water. The pool may then become inhospitable due to temperature increases or by slowly draining dry. Escape from these situations is cut off before there is a danger for the fish to react to, and therefore there is a selective advantage to possessing tidal rhythms especially when coupled with homing behaviour.

With the generally subtidal nature of *P. laeta* and their prey no selective advantage of possessing a tidal rhythm would be apparent.

In many fish species diurnal changes in behaviour are likely to be coordinated by the daily light-dark cycle although there is frequently an endogenous component which may be entrained (Woodhead 1966). Entrainment may be expressed by prefeeding behaviour just before the time that food is usually taken, even in the absence of usual daylight changing cues as demonstrated for bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) (Davis 1964), tomcod (*Microgadus tomcod*), scup (*Stentomus versicolor*) and killifish (*Fundulus heteroclitis*) (Davis and Bardach 1965). This phenomenon, if present in *P. laeta* and *P. ornata*, would account for the peaks in activity of both species during the time of anticipated dawn under constant dark conditions. The absence of a pronounced peak at dusk under constant dark indicates that a prefeeding peak was not recorded at that time. Food quantification results support these observations that prey is not likely to be taken at night and it is probable that both *Pholis* species are selective visual daytime feeders as discussed by Caine (1979). The evening activity peak may relate to movement of both species which is not accompanied by feeding.

Overlaps in the average activities are of similar magnitude to the subtidal habitat overlaps, but are much higher than the intertidal overlap and the average food overlaps. The similarities of activity patterns therefore result in very little separation along this niche dimension.

Averaged niche breadth values show that the *P. ornata* rhythm was less pronounced than that of *P. laeta*. However, the order of increasing diversity was not consistent with respect to species and the main factor contributing to the larger overall breadth of activity in *P. ornata* was the smaller peak in activity at the time of anticipated dawn under the constant dark conditions. Perhaps the entrainment of the crepuscular activity is less pronounced in *P. ornata* than *P. laeta*.

Activity niche breadths for the 12 two hour time units are consistently larger than the average for any food type niche breadth measure for size groupings of either species. This suggests that the food utilization of both species is more specialized than their activity patterns given the assumption of equal distinction between the dimension subdivisions.

Overall Relationship of Niche Measures

The niches of *P. laeta* and *P. ornata* are separated to the largest extent by low overlap of food use. The food types responsible for the greatest separation are located in distinct microhabitats within the eelgrass bed, although there are prey captured by *P. ornata* that are not restricted to the eelgrass beds.

The second most important dimension is the use of habitat which varies with tide height from an average overlap of 0.89 at low tide to 0.64 x 0.89 at high tides.

Temporal differences and food size differences appear to be of least importance based on the correlations between the species' use along these dimensions.

P. ornata show greater use of the habitats examined during the summer, greater variation in food type taken within fish size classes, plus greater variability in activity rhythm and therefore have a wider niche than *P. laeta*. *P. laeta* vary more than *P. ornata* in the scope of food size taken by the total of all fish size classes, due to the greater range of fish sizes and the correlation of food size with fish size.

Life History

Growth

P. laeta have been quoted to grow to a length of 10" (250 mm) (Clemens and Wilby 1961, Hart 1973, Somerton and Murray 1976, Eschmeyer *et al*. 1983) and *P. ornata* to a length of 12" (305 mm)(Hart 1973, Fitch and Lavenberg 1975, Somerton and Murray 1976, Eschmeyer *et al*. 1983). However, I did not catch fish of either species of lengths approaching these even though I believe the sampling would have captured them. Unless there is a change of habitat sought by *Pholis* at the largest sizes I believe that neither species grows to their reported maximum length in Saanich Inlet.

Growth rates of cohorts of *P. laeta* and *P. ornata* do not differ markedly in Saanich Inlet. This is based on the confirmation of assumed cohort ages by otolith analysis, and the fact that the estimate of age composition is not greatly affected by the choice in cut off values (Hasselblad 1966, Hosmer 1973) or normality of length distribution (McNew and Summerfelt 1978).

The oldest and largest *P. ornata* were captured in May of 1980 and were in their third year. As fish of this size class were not subsequently captured I suspect that *P. ornata* in Saanich Inlet are usually $2^1/_2$ years of age or younger. This is much younger than the longevity of 7 years suggested by Fitch and Lavenberg (1975) for the species in California.

Growth rates in Saanich Inlet for *P. ornata* are much faster than in Oregon. Barton (1982) found it increasingly difficult to separate young of the year *P. ornata* from older individuals as young grew to 45 mm in length by the end of the summer. These Oregon lengths are therefore smaller than the 50-80 mm lengths in Saanich Inlet, where young of the year were clearly identifiable from the older fish. Perhaps the settling of *P. ornata* in the rocky intertidal of Yaquina Bay results in fish feeding in a less productive environment than the eelgrass from where I collected them.

The greater maximum length observed for *P. laeta* compared to *P. ornata* is due to many individuals living at least one year longer than *P. ornata*. It is possible that increased mortality of *P. ornata* is associated with breeding activity. In both species breeding occurs after the second year. In Mill Bay, the number of *P. ornata* in their third year was 5% of the number in their second. The number of *P. laeta* in their third year was 38% of the number in their second. As the size of the fish are similar, and the size of *P. ornata* averages larger than those of comparable age in Yaquina Bay, it is unlikely that size dependent mortality or poor nutrition is a factor. Perhaps *P. ornata* are more exposed than *P. laeta* to predators in their search for breeding habitat in B.C. It is unlikely that *P. ornata* are semelparous and naturally die off after breeding in British Columbia because this would be a radically different life history strategy than in California where members of the species breed first after the second winter, have parental guarding of the eggs, and live up to 7 years (Fitch and Lavenberg 1975).

Mortality Curves

Assuming that the largest *Pholis* were captured I believe that the mortality curves and inferred number of young of the year are realistic. Based upon an average of 25 female *P. laeta* of 120 mm SL in the eelgrass area sampled and their average fecundity of 1200 eggs an expected 30,000 larvae would result. Knowing *P. laeta*'s nearby breeding location and the substrate settling preference for vegetation of this type (Marliave 1977) it seems likely that many larvae would settle in the area. Even if 10% of the larvae settled in the area and suffered logarithmic mortality between egg production and settling, the resulting number would still be higher then the 405 projected to be in the area:

$$\frac{\text{antilog}((\log 30{,}000) - 0.8)}{10} = 475$$

I believe that my estimation of *P. laeta* young is not overinflated and the weighting of the young of the year class, which reduce the WPC and increase the weightings of the young of the year prey utilization, is approximate.

As mature *P. ornata* females were not obtained in the study, fecundity estimates are not available. However, the lack of *P. ornata* of the sizes of largest *P. laeta*, and the fact that fecundity is correlated with size suggests that *P. ornata* are less fecund. As *P. ornata* are less abundant, it is evident that fewer young of the year would occur in the sampling area (as calculated by estimation of young of the year).

Breeding Behaviour of P. laeta

The breeding behaviour of *P. laeta* observed in this study is in general agreement with the parental care patterns noted in the pholididae (Gudger 1927, Qasim 1956, Norman and Greenwood 1963, Breder and Rosen 1966, Fitch and Lavenberg 1975, Marliave and De Martini 1977) with few additions. The breeding colouration of male fish suggests that it might be important in the recognition of the sexes and possibly mate choice. As pairing occurs with usually only one breeding pair under each rock there is likely to be a preference for this situation or some defense of the area from other adults. This seemingly does not extend to juveniles or other fish species, notably *Anoplarchus purpurescens* which were commonly found with breeding *P. laeta*.

The occurrences of *P. laeta* under rocks on a firm sandy bottom demonstrates that interstitial spaces are not always required before the rock is selected. *P. laeta* can obviously excavate a small interstitial space under the rock, and the pathway opened may then be filled in by shifting sand washed by waves. This is quite different from the substrates selected by *Xiphister atropurpureus* where substrates of sand under rock are unsuitable for spawning (Marliave 1975). Coincidentally *X. atropurpureus* occur in local waters outside of Saanich Inlet where siltation is less of a problem.

Reports (Marliave and Demartini 1977) that two *P. laeta* wrap around the egg mass simultaneously are correct, but not all of the time. Field observations demonstrate incidences of one *P. laeta* with an egg mass. Additionally, aquarium observations show that the egg mass is not always guarded by both parents although this may be due to an unnatural laboratory situation. However, even with inconsistent guarding, 4 out of 5 egg masses hatched and so it is unlikely that the parents must provide much consistently active care for the eggs. No fanning of eggs was observed, nor is it reported by other researchers. Guarding probably protects the egg masses from predation, or from becoming dislodged by waves into a more dangerous environment since the eggs are not attached to the cover or the substrate.

Large environmental fluctuations characterize the intertidal breeding habitats at Patricia Bay. Extreme tide changes in January result in intertidal breeding fish being exposed to temperature changes from 6°C surface water to −8°C air temperature on some occasions as well as salinity changes of 8°/oo surface to

22°/oo when immersed in 2 m of depth. Although the interstitial fluctuations may be more moderate, both *P. laeta* and their eggs must be tolerant of marked changes.

SUMMARY

1. *P. laeta* and *P. ornata* coexist in Saanich Inlet eelgrass beds during the summer but are absent during the winter.
2. Summer habitat use is subdivided for *Pholis* of one year of age and older. *P. laeta* are evenly distributed in the subtidal eelgrass zone and do not venture to a large extent into the intertidal zone at high tide. *P. ornata* show peak abundances in the shallowest water at low tide and occur intertidally at high tide in numbers disproportionately high relative to *P. laeta*.
3. Some young of the year of both species occur entwined around eelgrass blades in the canopy.
4. Diet of the young of both species consists mainly of harpacticoid copepods.
5. Adult *Pholis* show interspecific reduction in overlap of food resources. *P. laeta* capture many prey located on the *Zostera* blades. *P. ornata* feed on many benthic organisms and take a greater diversity of prey types than do *P. laeta*.
6. As a species, *P. laeta* feed on a wider range of prey sizes than *P. ornata* due to a larger size range. In small size classes *P. ornata* take a wider variety of prey sizes. There is no significant difference between the species in mean food size taken.

7. Both species show peaks in laboratory activity at dusk and dawn under photoperiod conditions and at the time of anticipated dawn under constant dark conditions.
8. Field feeding patterns are not solely influenced by tide height. More feeding occurs during early morning than at night.
9. Separation of habitat occurs during the winter when *P. laeta* of 2 years of age and older spawn under rocks in the intertidal and shallow subtidal regions. Breeding locations of *P. ornata* were not observed.
10. Mature *P. laeta* males develop breeding colouration during the winter. Spawning occurs in late January with eggs hatching in March. Guarding of the egg mass was inconsistent and not mandatory for hatching under laboratory conditions.
11. *P. laeta* and *P. ornata* show similar growth rates but *P. ornata* is less common and shorter lived than *P. laeta* in Saanich Inlet.
12. Niches are separated most by food differences, secondly by habitat differences and least by activity differences.
13. Overall, *P. ornata* has a wider niche and is less of a specialist than *P. laeta*.

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APPENDIX 1

List of fish species collected from the subtidal eelgrass bed at Mill Bay and Patricia Bay during 1980.

Listed in decreasing order of frequency of occurrence in any number.

	MILL BAY												PATRICIA BAY											
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Syngnathus leptorhynchus	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X		X	X
Cymatogaster aggregata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X	X		X
Leptocottus armatus	X	X	X	X	X	X			X	X	X	X	X	X	X	X		X	X	X	X	X		X
Artedius fenestralis	X	X			X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X		X
Pholis laeta				X	X	X	X	X	X	X			X	X			X	X	X	X	X	X	X	X
Hexagrammos stelleri	X	X	X	X	X	X	X	X	X	X	X	X				X	X	X			X			
Pholis ornata			X		X	X	X	X	X	X			X				X	X	X	X	X	X		X
Platichthys stellatus	X	X		X							X	X	X	X	X	X	X	X	X	X		X		X
Gasterosteus aculeatus	X	X	X	X						X	X		X	X	X		X	X		X		X	X	X
Porichthys notatus	X	X			X		X		X				X	X	X	X	X	X	X	X	X			
Myoxocephalus polyacanthocephalus	X	X	X	X	X	X		X			X		X	X	X									X
Lumpenus sagitta			X			X	X		X						X	X	X	X	X	X	X	X		
Aulorynchus flavidus	X	X	X				X	X			X	X	X	X		X		X						X
Apodichthys flavidus				X	X	X	X	X	X	X	X								X	X	X			
Embiotoca lateralis							X	X	X	X			X	X	X		X	X	X					X
Parophrys vetulus	X	X	X			X	X	X			X	X					X	X						
Rhacochilus vacca	X					X		X	X			X	X	X	X					X	X			
Enophrys bison	X	X	X		X	X							X	X							X			X
Lepidogobius lepidus													X	X	X		X	X		X		X	X	X
Oligocottus maculosus	X	X		X		X	X											X	X	X	X			
Anoplarchus purpurescens	X	X	X					X					X	X				X	X	X				X
Clinocottus acuticeps		X					X	X						X			X	X	X					
Blepsias cirrhosus				X	X		X	X	X						X			X						

APPENDIX 1 (continued)

	MILL BAY												PATRICIA BAY											
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Oncorhynchus keta			X	X	X										X	X	X							
Pleuronichthis coenosus							X	X		X	X					X		X						
Ophiodon elongatus	X	X		X						X	X	X												
Chitonotus pugetensis	X	X	X	X									X											
Liparis sp					X								X	X										X
Sebastes juvenile							X	X		X								X						
Agonus acipenserinus	X	X	X																					
Clupea pallasi											X	X	X											
Scorpaenichthys marmoratus	X	X																						
Artedius lateralis													X						X					
Nautichthys oculofasciatus					X			X																
Pallasina barbata aix																			X			X		
Hypomesus pretiosus pretiosus		X																						
Agonopsis emmelane	X																							
Rhamphocottus richardsoni													X											
Ammodytes hexapterus				X																				
Lepidopsetta bilineata																X								
Theragra chalcogramma	X																							
Microgadus proximus	X																							
Psychrolutes paradoxus	X																							
Xiphister atropurpureus								X																

APPENDIX 2

WATER TEMPERATURES AND SALINITY AT MILL BAY AND PATRICIA BAY DURING 1980

		Mill Bay		Patricia Bay	
	Depth (m)	Water Temperature (°C)	Salinity (°/oo)	Water Temperature (°C)	Salinity (°/oo)
JANUARY	surface	7.5	25.0	4.0	8.0
	-1	8.0	27.0	5.0	20.5
	-2	8.0	27.5	6.0	22.0
FEBRUARY	surface	5.0	19.0	6.5	26.0
	-1	5.0	21.0	7.0	28.0
	-2	6.0	27.0	7.5	28.5
MARCH	surface	6.0	29.0	7.0	27.0
	-1	7.0	28.5	7.5	26.5
	-2	7.0	29.0	7.0	26.5
APRIL	surface	12.5	23.5	10.0	27.5
	-1	10.0	24.0	9.5	27.5
	-2	9.5	24.0	9.0	28.0
MAY	surface	16.5	24.0	14.5	25.5
	-1	15.0	25.0	13.5	26.5
	-2	14.0	26.0	12.5	27.0
JUNE	surface	17.5	25.0	17.0	25.0
	-1	16.5	26.0	15.0	26.0
	-2	15.0	27.0	14.5	26.5

JULY (over)

APPENDIX 2 (contd)

WATER TEMPERATURES AND SALINITY AT MILL BAY AND PATRICIA BAY DURING 1980

		Mill Bay		Patricia Bay	
	Depth (m)	Water Temperature (°C)	Salinity (°/oo)	Water Temperature (°C)	Salinity (°/oo)
JULY	surface	19.0	22.0	11.0	31.5
	-1	17.0	23.5	10.0	32.0
	-2	16.0	23.5	9.5	31.5
AUGUST	surface	15.5	26.0	15.0	25.0
	-1	15.5	25.0	14.5	24.0
	-2	14.0	26.0	14.5	23.5
SEPTEMBER	surface	15.0	22.5	12.5	27.0
	-1	14.0	23.5	12.5	27.0
	-2	13.0	24.5	12.5	27.0
OCTOBER	surface	10.0	26.0	10.5	26.5
	-1	10.0	26.0	10.5	27.0
	-2	10.0	26.5	10.5	27.0
NOVEMBER	surface	6.0	12.0	5.0	18.0
	-1	7.0	19.5	6.0	21.0
	-2	8.0	20.0	7.0	24.0
DECEMBER	surface	7.0	12.0	7.5	6.5
	-1	7.0	19.5	7.0	23.0
	-2	7.5	23.0	7.5	25.0

VITA

Surname: HUGHES Given names: GRANT WILLIAM

Place of Birth: Vancouver, B.C. Date of Birth: 2 May 1954

Educational Institutions attended, with dates of entering and leaving:

University of Calgary 1972 to 1973

University of Victoria 1973 to 1976

University of Victoria 1980 to 1983

Degrees, Diplomas, Etc., Awarded, with dates and names of Institutions:

B.Sc.	1976	University of Victoria

Honors and Awards:

Publications:

Peden, A.E. and Grant W. Hughes. 1981. Life history notes relevant to the Canadian status of the speckled dace (*Rhinichthys osculus*). Syesis 14: 21-31.

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