



Variations of life history parameters in two geographical groups of the neon flying squid, *Ommastrephes bartramii*, from the North Pacific

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Abstract

The neon flying squid, *Ommastrephes bartramii* (Lesueur), is a widespread subtropical to temperate species, and is composed of several tempo-spatial groups in the North Pacific. We analyze the growth parameters of two allopatric stocks with two seasonal cohorts using statolith microstructure, and propose a tempo-spatial migration model.

We used 571 statoliths, obtained from juvenile/adult squids (175–527 mm mantle length, ML). Based on precise digitized statolith growth marks, various early life demographic traits were estimated by the back-calculation method. Two cohorts of autumn and winter were identified in the northeastern (NE) North Pacific, while only a comparable winter cohort was found in the northwestern (NW). There was a significant difference in the relationships of statolith radius (Ra) to increment numbers (In) between NE and NW stocks. However, linear ML to Ra relationship exhibited no geographic difference in large females (>350 mm ML), but significant difference between NE and NW in both small females (<350 mm ML) and males. Growth in length (ML) at week (t) is best fitted by a power function of innate growth for NE small females and males, and NW large females; however, the Gompertz function of decreasing growth rate is better for NE large females, and NW small females and males. Variations on demographic traits confirm two geographic stocks of NE and NW, and two seasonal cohorts of NE stock. Indistinguishable growth parameters shown by NE and NW large females suggest a longer life history of the population, which migrates across the geographic boundary at a longitude of 170°E. The ambient temperature, that corresponding to their early life stages, could be a plausible factor in later growth difference.

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1. Introduction

The neon flying squid, *Ommastrephes bartramii* (Lesueur), is an oceanic schooling cephalopod occur-

ring in subtropical and temperate waters of the world (Roper et al., 1984). In the North Pacific, commercial fishing targeting this species started in 1974 as a substitute for the then sharply collapsed fishery of *Todarodes pacificus* (Araya, 1983). Annual production was estimated at 200,000–300,000 mt by high sea drift netters in the 1980s and ca. 50,000 mt by jiggers in the 1990s (FAO, 2001). The fishing ground used by most fishermen is divided geographically into

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northeastern (NE) and northwestern (NW) North Pacific. Despite the importance of the neon flying squid fishery and the sensitive fluctuating recruitment of the squid population (Anderson and Rodhouse, 2001; Rodhouse, 2001), there is no appropriate organization to undertake stringent assessment and management of the fishery.

The population structure of *O. bartramii* is unclear for the purpose of fisheries management, but at least two putative seasonal cohorts, autumn-breeding and spring-breeding, have been suggested (Murakami et al., 1981; Murata, 1990). Multiple seasonal cohorts resulted in size variations and that had been found within a categorized catch composition (Murata, 1990). A higher proportion of females over males was found in larger size group (>350 mm ML). Based on statolith microstructure analysis, Yatsu et al. (1997) concluded that *O. bartramii* spawned almost year round, and the life span was probably 1 year.

Juvenile *O. bartramii* recruit to the fishery at a size of 150–170 mm ML (Murata, 1990). Asymptotic growth pattern has been estimated by using monthly time series of ML (Murakami et al., 1981; Welch and Morris, 1993). However, growth functions estimated from length-based methods are considered inappropriate for fast-growing and temperature dependent squids (Forsythe, 1993; Jackson et al., 1997, 2000), especially for those species undertaking large-scale migrations across subtropical-temperate waters (Caddy, 1991). Statolith microstructure was found to be a useful and precise tool for age determination in squids (Rodhouse and Hatfield, 1990; Jackson, 1994) and hence for development of more robust demography. By reading statolith growth increments, Bigelow and Landgraf (1993) parameterized exponential growth of *O. bartramii* paralarvae from hatching to 35 days. Putting prevailing current information together, Bower (1996) inferred the hatching ground of *O. bartramii* to be in the Hawaiian waters. Yatsu and Mori (2000) reared paralarvae and extrapolated the findings to wild juveniles to assume that the neon flying squid grows exponentially in paralarvae stage and linearly in juvenile. However, the variations of growth pattern between seasonal cohorts are still unclear.

In general, the squid statolith enlarges with body size by adding calcium carbonate and organic materials onto the outer rim of the existing structure (Lipinski, 1993; Bettencourt and Guerra, 2000). Anal-

ysis on statolith microstructure is therefore a convenient method for retrogressive estimation of early life traits. Back-calculation method has been used for fitting appropriate growth curves in fish, and allowed for the estimation of sizes at ages that are uncommon or difficult to collect (Francis, 1990; Secor and Dean, 1992). The statolith in cephalopods is similar to a fish otolith, but its technique for age determination is still under exploration. In this study, we hypothesize two geographic stocks of *O. bartramii* in the North Pacific, recognize two seasonal cohorts, and apply intensive statolith microstructure analysis to elucidate growth difference between the groups.

2. Materials and methods

2.1. Squid sampling

Samples of *O. bartramii* were collected from a survey by a chartered boat from 5 July to 17 August 1997 (38–45°98'N, 150–170°W), and from a commercial vessel during July–September 1998 (40°53'–45°11'N, 157°58'E–179°08'W) (Fig. 1). Samples from the chartered boat were taken daily, while samples from the commercial vessel were collected randomly from the monthly catches. Specimens were frozen on board immediately, and brought back to the laboratory for further processing. The basic information are showed in Table 1.

In the laboratory, squids for age determination were sub-sampled randomly from the collection. Sampled squids were thawed, dissected, and measurements of mantle length (ML) taken to the nearest 1 mm and body weight (BW) to 1 g. Dissected specimens were sexed, and sexual maturity staged followed Yatsu et al. (1998) (A: juvenile; B: maturing; C: mature; D: spent), and their statoliths were extracted.

2.2. Statolith preparation and increments reading

Each statolith was embedded in resin, cut to an appropriate size, and mounted on a glass slide. A thin longitudinal section of the statolith was obtained for observation. The prepared statoliths were examined under a compound microscope (Olympus Model BX50) with a C-mounted CCD camera. For each frame of a processed statolith image that was

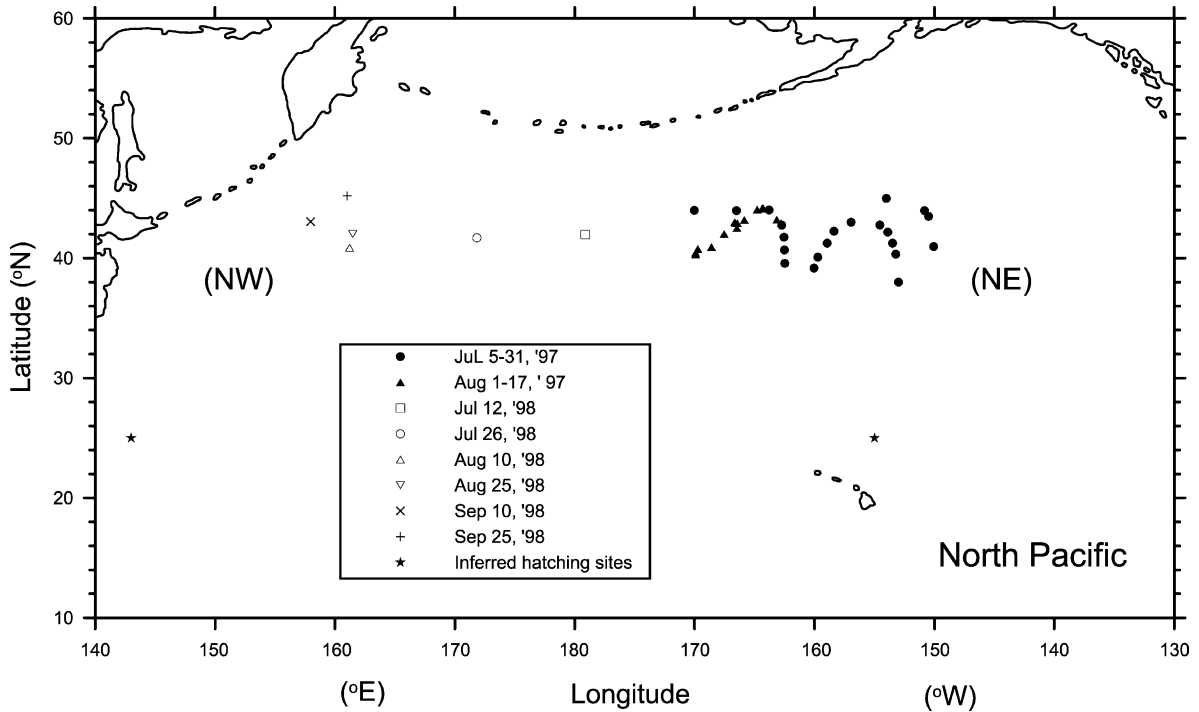


Fig. 1. Sampling localities of *O. bartramii* in the North Pacific.

needed, a clear picture was printed on thermal paper (SONY UP-860). Multiple frames of a statolith image were stitched together as a whole (Fig. 2), and the growth increments of the statolith were determined and marked on a superimposed transparency sheet on the longest axis from the focus to the edge of dorsal dome. Coordinates (*x*, *y*) of the increment landmarks

were digitized, and stored in an electronic file. Increment size, *I_n* (distance between two neighboring rings) and ring radius, *R_a* (distance from focus to a specific ring) were calculated.

The temporal formation of growth increments in statoliths of *O. bartramii* has not been validated with direct observation. Yet, Yatsu et al. (1997) suggested

Table 1
Sampling date, locality, sample size, ML (mm), BW (g), and increment number of *O. bartramii* examined in this study

Year/date	Latitude	Longitude	Sample size (F, M)	ML (mm)	BW (g)	Increment number
1997						
5–31 July	38°00′–43°59′N	150°04′–170°02′W	161, 8	175–505	126–4627	181–370
1–17 August	40°19′–44°11′N	162°48′–169°55′W	126, 35	181–527	147–5017	183–356
1998						
12 July	41°58′N	179°08′W	22, 0	360–437	1457–2762	252–318
26 July	41°42′N	171°50′W	24, 0	357–430	1427–1932	243–324
10 August	40°53′N	161°13′E	17, 50	195–268	196–500	219–312
25 August	42°01′N	161°29′E	35, 33	203–287	235–687	240–339
10 September	43°28′N	157°58′E	29, 14	215–254	256–438	176–267
25 September	45°11′N	161°06′E	17, 0	387–493	1816–3714	256–367

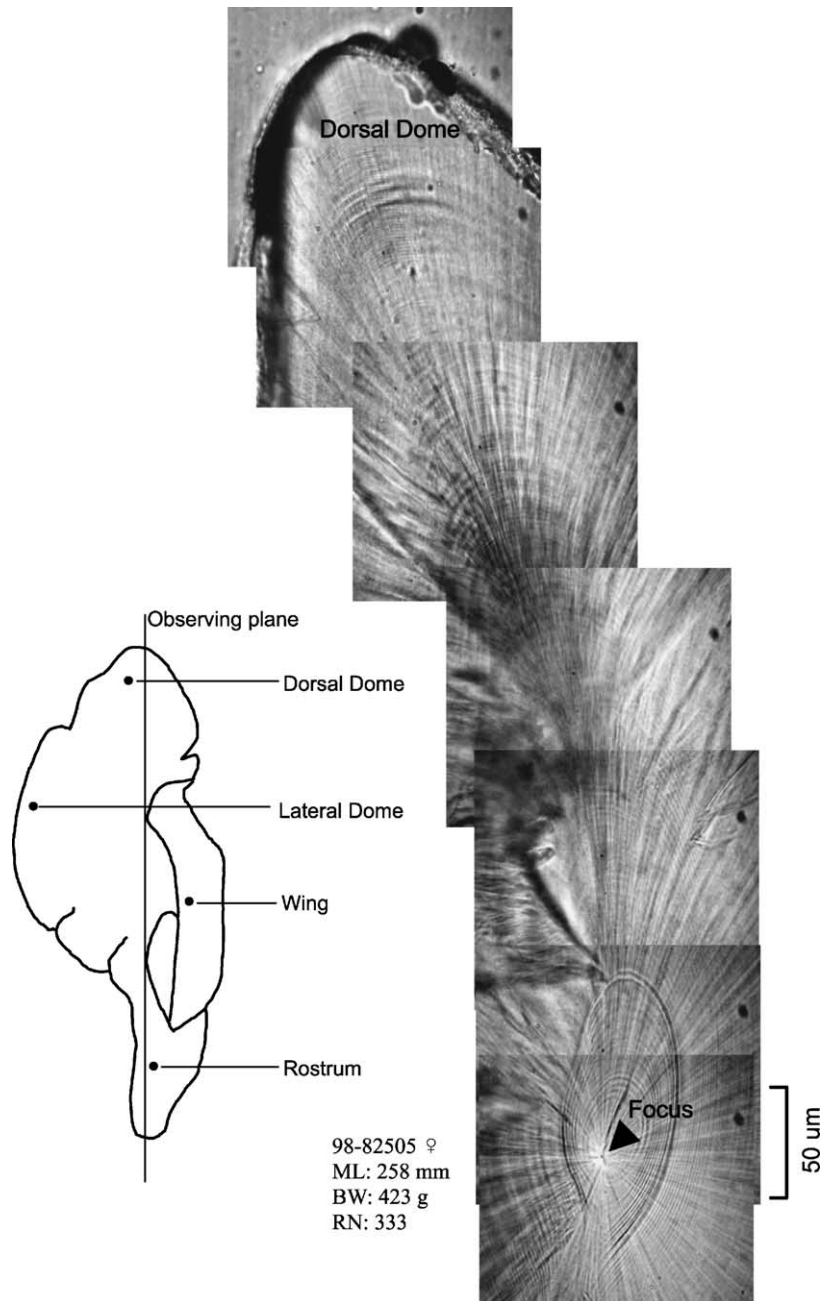


Fig. 2. A statolith of *O. bartramii* (female, 258 mm ML, 423 g BW and 333 days), showing a composite of seven reading frames in increments.

the deposition of growth increments occurs on a daily basis. We have therefore assumed that the growth increment of *O. bartramii* is daily. Accordingly, the total number of rings being digitized was considered to be equivalent to the age of the squid in days. Hatching date was determined by subtracting estimated daily ages from the date of capture.

2.3. Back-calculated size-at-age data

The ML-at-age data of *O. bartramii* were back-calculated by the biological intercept method (Campana, 1990). The equation is

$$L_a = L_c + \frac{(O_a - O_c)(L_c - L_o)}{O_c - O_o},$$

where L_a and O_a represent ML and statolith radius at age a , L_c and O_c are those at capture, and L_o and O_o are biological intercepts. For *O. bartramii*, ML at hatching was 1.139 mm and statolith radius was 11.914 μm (Yatsu and Mori, 2000). The BW-at-age was converted from the ML–BW relationship, which was estimated allometrically, $\text{BW} = a \text{ML}^b$.

Possible growth patterns of *O. bartramii* were trialed by fitting size-at-age (L_t , mm) and age data (t , weeks) to various functions, and power ($L_t = at^b$) and Gompertz function ($L_t = L_0 \exp(G(1 - e^{-gt}))$) were selected by the highest value of coefficient of determination (R^2). Specific growth rates (SGR, mm or g per day) were estimated for each 14-day interval. The estimator for SGR is: $\text{SGR} = (S_2 - S_1)/\Delta T$, where S_1 and S_2 are estimated ML or BW values at the beginning and end of the time interval (Ricker, 1958). Statistical procedures were performed using the statistical package SAS (SAS Institute, 1989).

The geographic stocks of NE and NW were delimited by 170°E (Yatsu et al., 1998). Female and male were treated separately. Females of ML greater than 350 mm were separate into different groups, which was treated as autumn cohort in NE (Murata, 1990; Yatsu et al., 1997). We adopted an ANCOVA model to test the difference on demographic traits, with the geographic stocks (NE and NW) and sexes as four major groups (2×2), plus part of female samples could be further grouped into large and small defined by a ML of 350 mm (2×3). No size group was applied to the males because of the absence of large squid (>350 mm ML) in exploitation phase.

2.4. SST data

The sea surface temperature (SST) at the estimated hatching ground of *O. bartramii* were obtained from the GlobalSST data set, which contains monthly optimum interpolation (OI) SST images in Idrisi format. The image frames of monthly SST were converted to ASCII data file using ‘CONVERT’ procedure of Idrisi32 package (Idrisi32, Release 2, Clark Labs, Clark University). The spatial resolution is 1° of latitude and longitude. The hatching region was found likely to be 25°N, 143°E and 25°N, 155°W based on hatching dates, presumed migratory routes and collecting sites of *O. bartramii* paralarvae (Okutani, 1968; Young and Hirota, 1990; Hayase, 1995; Bower, 1996).

3. Results

3.1. Hatch date distribution

We examined 571 statoliths of *O. bartramii*, which indicated a hatching period of over 8 months from August to the next March (Fig. 3). The NW group females hatched from September to March; with large-sized group (NW-L) peaking in December, while small-sized (NW-S) peaked in November and February. The hatching of NE group females was estimated from August to February; with large-sized squids (NE-L) peaking in October (autumn cohort), while small-sized (NE-S) peaked in December (winter cohort). This NW pattern differed from that of NE geographic group, such that a comparable winter cohort was confirmed but no indication of autumn cohort. All male squids hatched during October–February, and peaked in December for NE group and in November for NW group.

3.2. Statolith growth

Statolith radius, measured from focus to outer edge of dorsal dome, ranged from 476 μm (male, 212 mm ML, maturing) to 898 μm (female, 475 mm ML, maturing). The statolith radius (Ra) in relation to increment numbers (In) could be estimated linearly in both sexes. Size difference of Ra–In relationship was found in NW samples: $\text{Ra} = 161.87 + 1.99 \text{In}$ ($n = 17$, $r =$

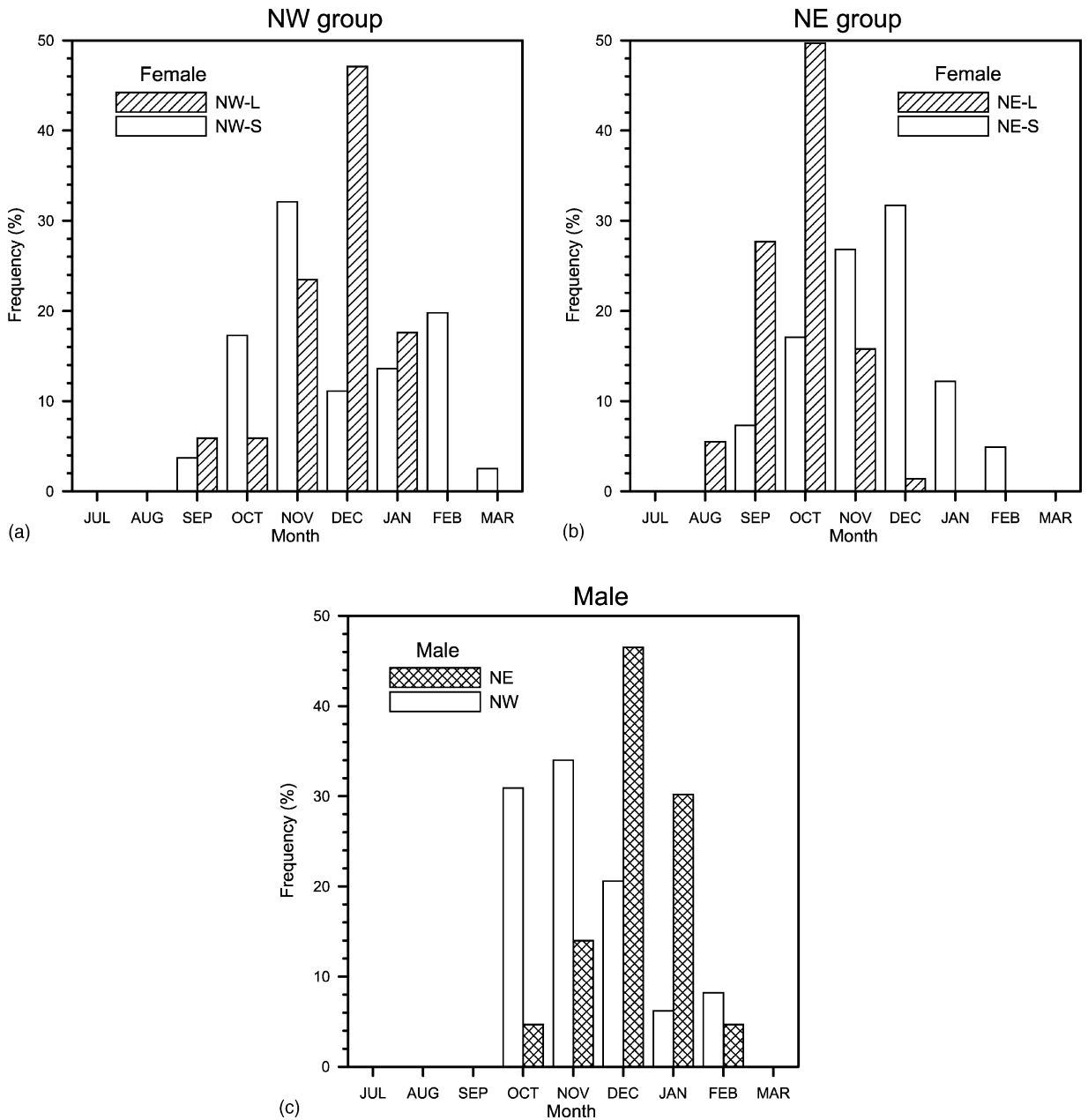


Fig. 3. Distribution of back-calculated hatching dates of *O. bartramii* in the North Pacific: (a) NW female; (b) NE female; (c) male of NW and NE.

0.905, $P < 0.0001$) and $Ra = 434.47 + 0.57 \ln$ ($n = 81$, $r = 0.529$, $P < 0.0001$), for NW-L and NW-S groups, respectively (Fig. 4). For NE females, there was no significant difference in slope between NE-L

and NE-S groups ($P = 0.791$), and a common equation was obtained, $Ra = 155.32 + 1.97 \ln$ ($n = 333$, $r = 0.939$). For males, the relationships were $Ra = 129.33 + 2.01 \ln$ ($n = 43$, $r = 0.965$, $P < 0.0001$)

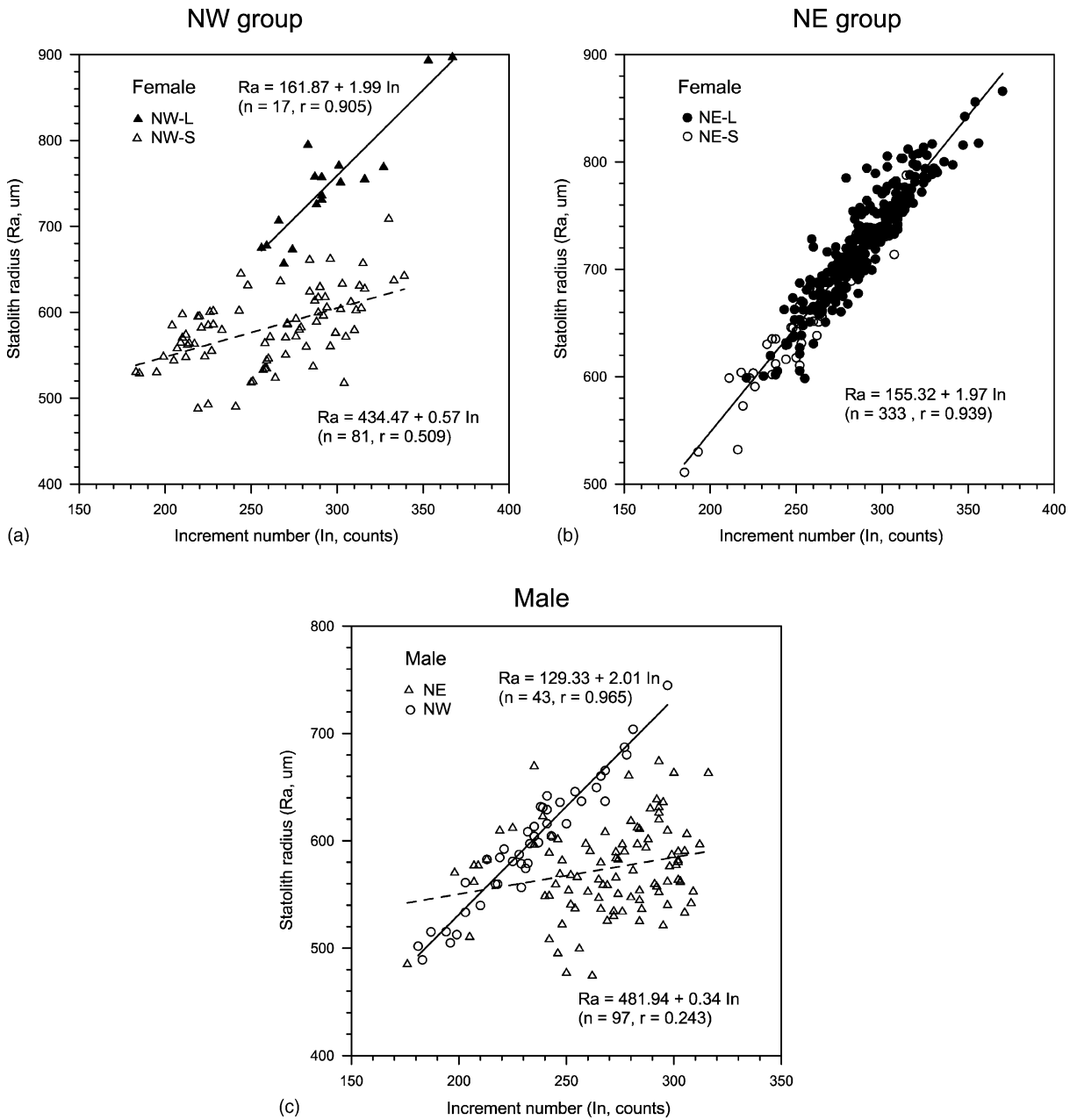


Fig. 4. Relationship between increment number, In (n) and statolith radius, Ra (μm) of *O. bartramii* in the North Pacific: (a) NW female; (b) NE female; (c) male.

and $Ra = 481.94 + 0.34 \ln$ ($n = 97, r = 0.243, P = 0.016$), for NE and NW, respectively.

The relative growth of ML to Ra could also be linear in both sexes (Fig. 5). For NW females, size dif-

ference was found in intercept ($P = 0.0006$), while not significant in slope ($P = 0.466$). The relationship were $ML = 275.72 + 0.21 Ra$ ($n = 17, r = 0.473, P = 0.055$) and $ML = 80.43 + 0.26 Ra$ ($n = 81, r =$

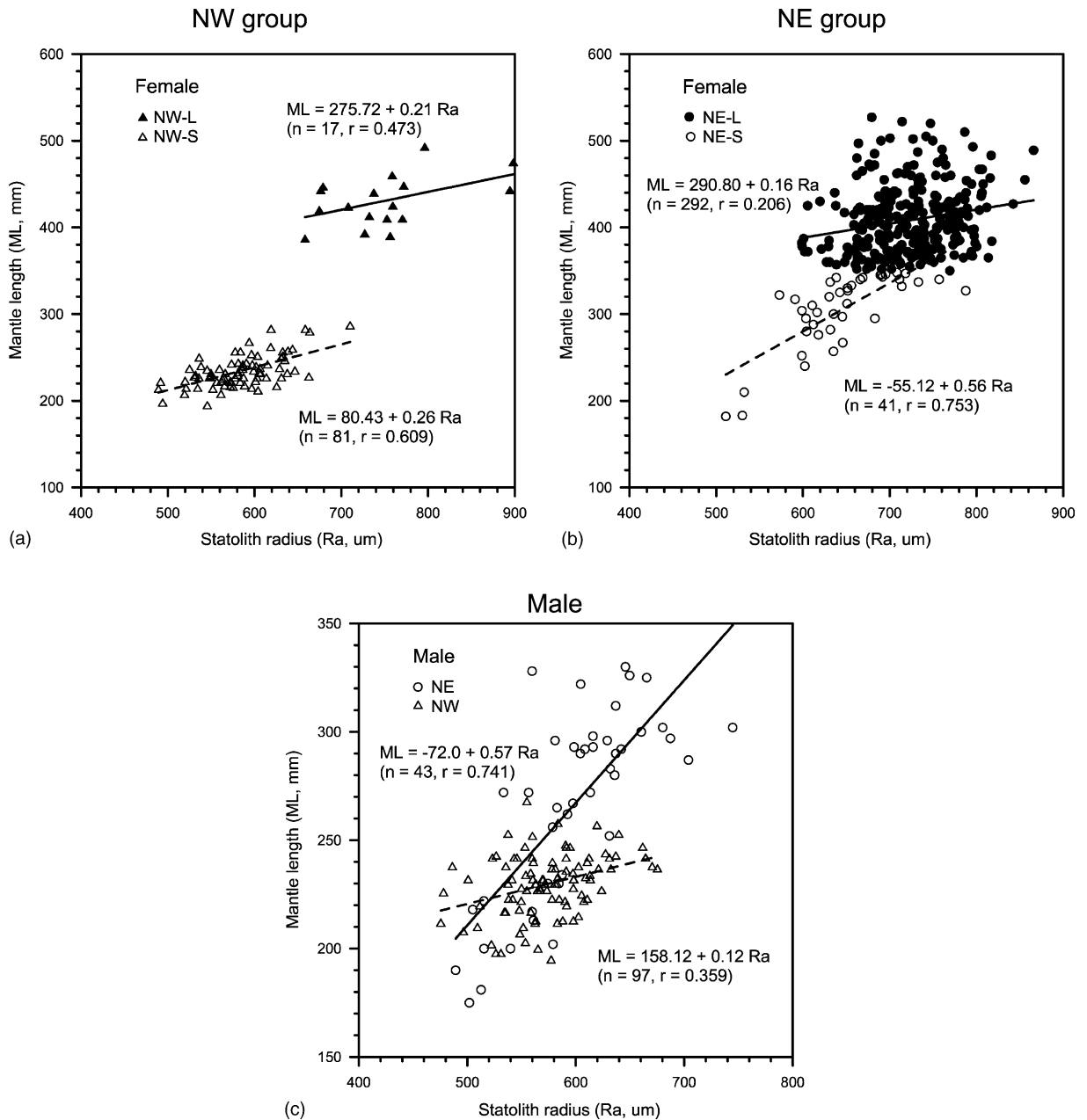


Fig. 5. Relationship between statolith radius, Ra (um) and ML (mm) of *O. bartramii* in the North Pacific: (a) NW female; (b) NE female; (c) male.

0.609, $P < 0.0001$) for NW-L and NW-S groups, respectively. For NE females, size difference was significant statistically ($P = 0.003$); $ML = 290.80 + 0.16 Ra$ ($n = 292$, $r = 0.206$, $P = 0.0004$) and $ML =$

$-55.12 + 0.56 Ra$ ($n = 41$, $r = 0.753$, $P < 0.0001$) for NE-L and NE-S groups, respectively. For males, this relationship was significantly different between NE and NW groups: $ML = -72.00 + 0.57 Ra$ ($n = 43$,

Table 2

O. bartramii: parameters for the relationship of back-calculated ML-at-age by geographic and sized groups in the North Pacific (NE-L: NE large group; NE-S: NE small group; NW-L: NW large group; NW-S: NW small group)^a

Groups	Growth function applied	Parameters			N	R ²
		a/L ₀	b/G	g		
Female						
NW-L	Power	20.032	0.819		42	0.9997
NW-S	Gompertz	22.020	2.484	0.070	44	0.9997
NE-L	Gompertz	40.200	2.470	0.063	47	0.9995
NE-S	Power	17.962	0.795		39	0.9998
Male						
NW	Gompertz	22.820	2.468	0.064	43	0.9997
NE	Power	20.238	0.740		38	0.9997

^a Power function: $L_t = at^b$; Gompertz function: $L_t = L_0 \exp(G(1 - e^{-gt}))$, where L is the back-calculated ML, t the age in weeks.

$r = 0.741$, $P < 0.0001$) and $ML = 158.12 + 0.12 Ra$ ($n = 97$, $r = 0.359$, $P = 0.0003$) for NE and NW groups, respectively.

3.3. Growth patterns

The BW–ML relationships of females *O. bartramii* are allometric $BW = 8 ML^{3.241} (10^{-6})$ ($n = 431$, $r = 0.976$), without geographical and size difference (ANCOVA, $P > 0.05$). However, geographic difference was found with males (ANCOVA, $P < 0.05$): $BW = 9 ML^{3.209} (10^{-6})$ ($n = 43$, $r = 0.991$) and $BW = 4.6 ML^{2.901} (10^{-5})$ ($n = 97$, $r = 0.954$), for NE and NW groups, respectively.

The growth of *O. bartramii* was estimated by back-calculated size-at-age data on a weekly basis. All parameters of growth functions applied are tabulated in Table 2 for ML and Table 3 for BW. The growth patterns of NE-L females, NW-S females and NW males were described by Gompertz function, while NE-S females, NW-L females and NE males by power function (Table 2 and Fig. 6). On the BW growth model, the Gompertz function was used for NE-L females, NW-S females and NW males, while power function was applied for NE-S females, NW-L females and NE males (Table 3 and Fig. 7).

Comparing growth trajectories, we found geographic difference was significant, that ontogenetic size in length differed as early as 1-week-old and in

Table 3

O. bartramii: parameters for the relationship of back-calculated BW-at-age by geographic and sized groups in the North Pacific (NE-L: NE large group; NE-S: NE small group; NW-L: NW large group; NW-S: NW small group)^a

Groups	Growth function applied	Parameters			N	R ²
		a/W ₀	b/G	g		
Female						
NW-L	Power	0.398	2.345		42	0.9998
NW-S	Gompertz	0.593	6.880	0.062	44	0.9989
NE-L	Gompertz	3.330	7.210	0.056	47	0.9996
NE-S	Power	0.058	2.721		39	0.9997
Male						
NW	Gompertz	0.398	7.148	0.066	42	0.9994
NE	Power	0.154	2.353		38	0.9998

^a Power function: $W_t = at^b$; Gompertz function: $W_t = W_0 \exp(G(1 - e^{-gt}))$, where W is the back-calculated BW, t the age in weeks.

weight not later than 8 weeks in both sexes. However, time series SGRs by ML (mm per day) showed a similar pattern in both sexes and geographical groups; a sharp decline was observed in the first 6–8 weeks, decreasing less during weeks 10–22 with high variation after approximately 28 weeks (Fig. 8). Initial SGR was apparently different between groups, and it was a determining factor in the final grouping. For example, a large female was 2.09 and 2.04 mm per day, while a small female was 1.71 and 1.21 mm per day for NE and NW groups, respectively. For small squid, the NE group had a higher SGR than that of NW group in both sexes of small-sized individual.

Squid gains BW rapidly after hatching, as shown by time series SGR (g per day) (Fig. 9). The increasing trend reached a peak at ca. 30 weeks, and then sharply decreased. Again, the NE group had a higher SGR than that of NW in general, except that large females (both in NE-L and NW-L groups) had almost the same pattern of growth.

4. Discussion

In this study, we back-calculated size-at-age data from growth increments of statoliths, and analyzed the growth patterns of six categorized samples from the North Pacific: two areas (NE and NW) \times 3 sex/size groups (large female (>350 mm ML), small female

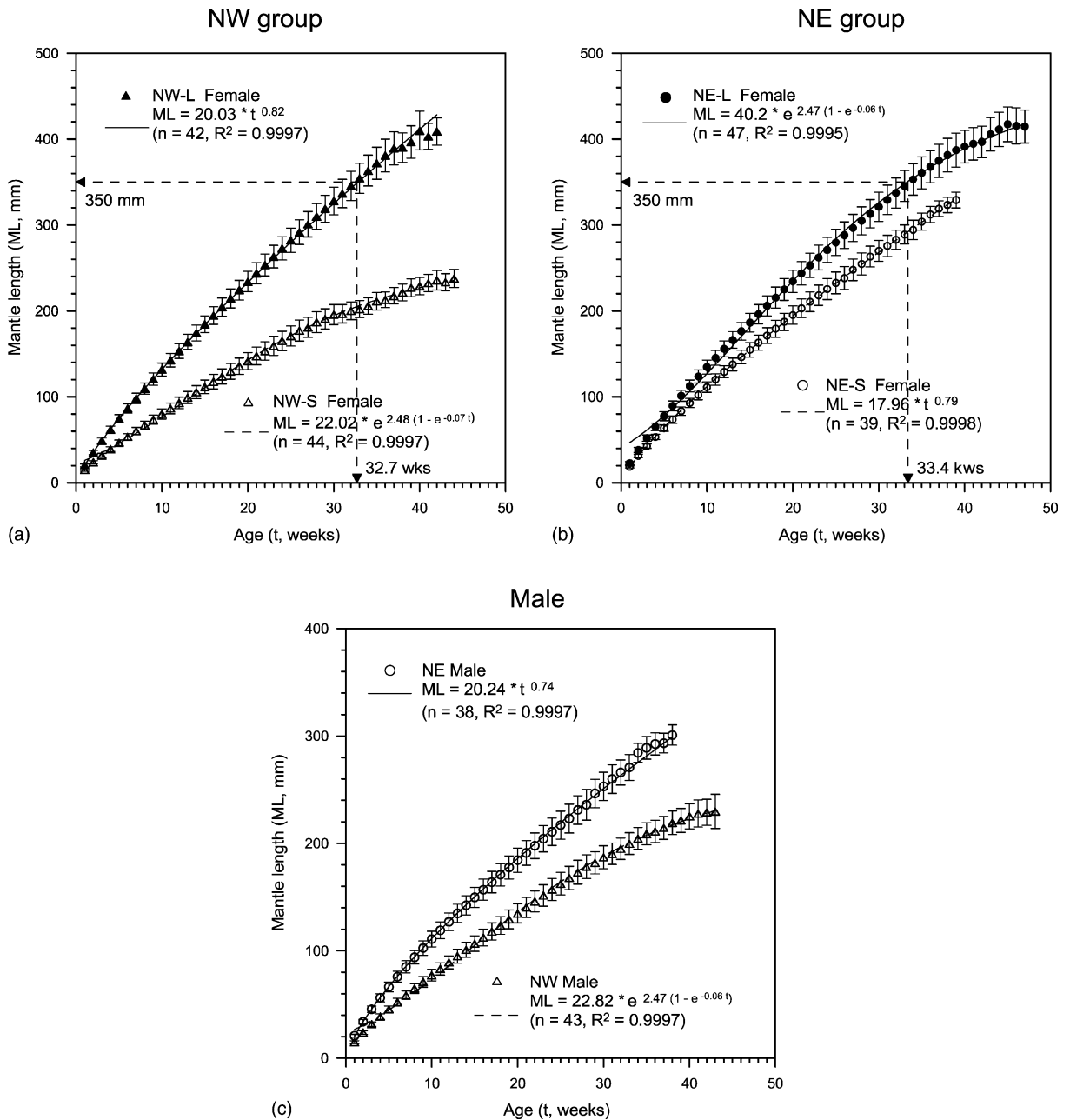


Fig. 6. Weekly back-calculated size-at-age (ML) and estimated growth functions of *O. bartramii* in the North Pacific: (a) NW female; (b) NE female; (c) male.

(<350 mm ML), and male). Our demographic analysis supports two geographic populations with two seasonal cohorts for *O. bartramii* in the North Pacific. This is the first attempt to obtain precise statolith read-

ings digitally and using a biological intercept method to reconstruct early growth of squids, which has been widely used in fish population analysis (Campana, 1990; Francis, 1990).

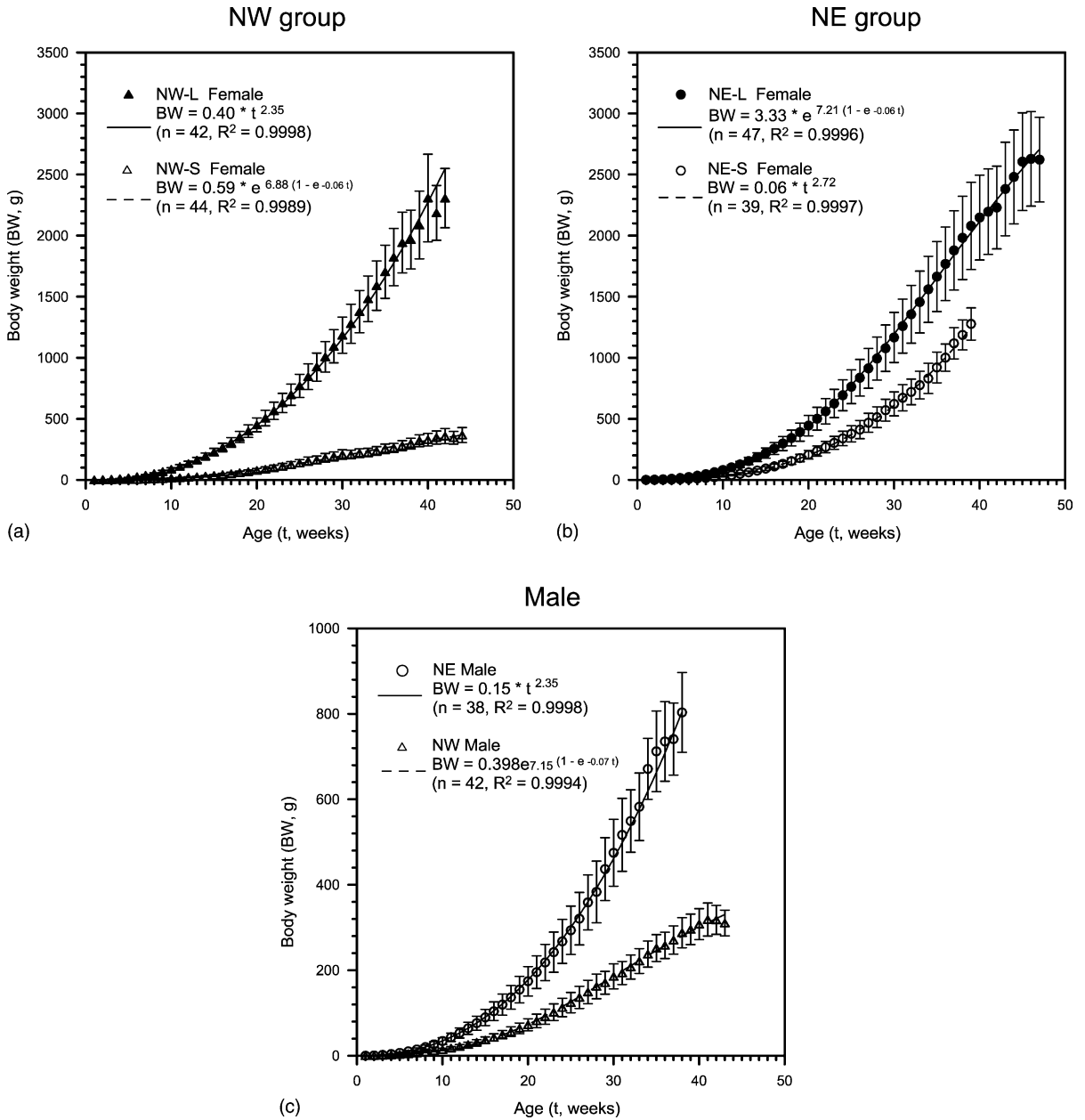


Fig. 7. Weekly back-calculated size-at-age (BW) and estimated growth functions of *O. bartramii* in the North Pacific: (a) NW female; (b) NE female; (c) male.

4.1. Population structure of *O. bartramii*

Two separate geographic fishing regions were experienced by the jigger fleet fishing on *O. bartramii*

in the North Pacific. The fishing season started in early May–June in the NE North Pacific, and then vessels moved to the NW during July–August. Our findings suggest that *O. bartramii* in the North Pacific

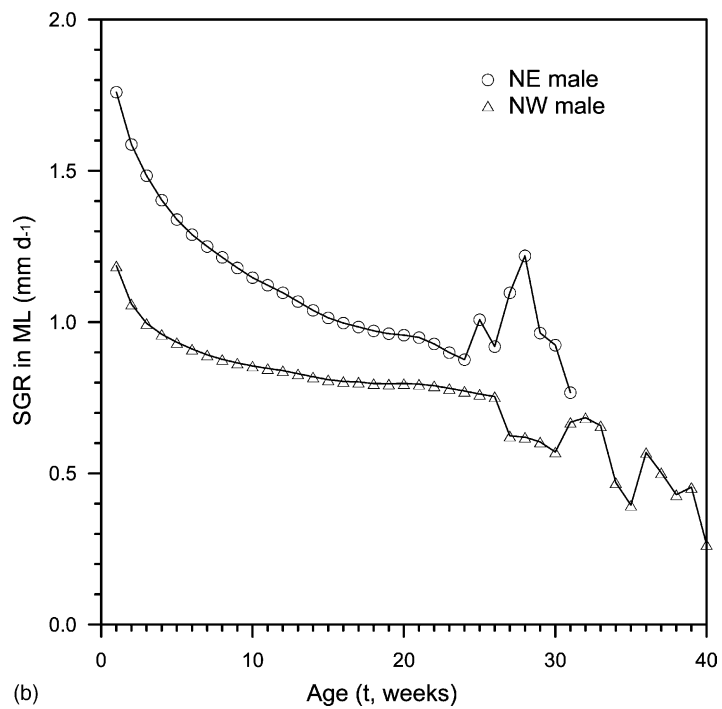
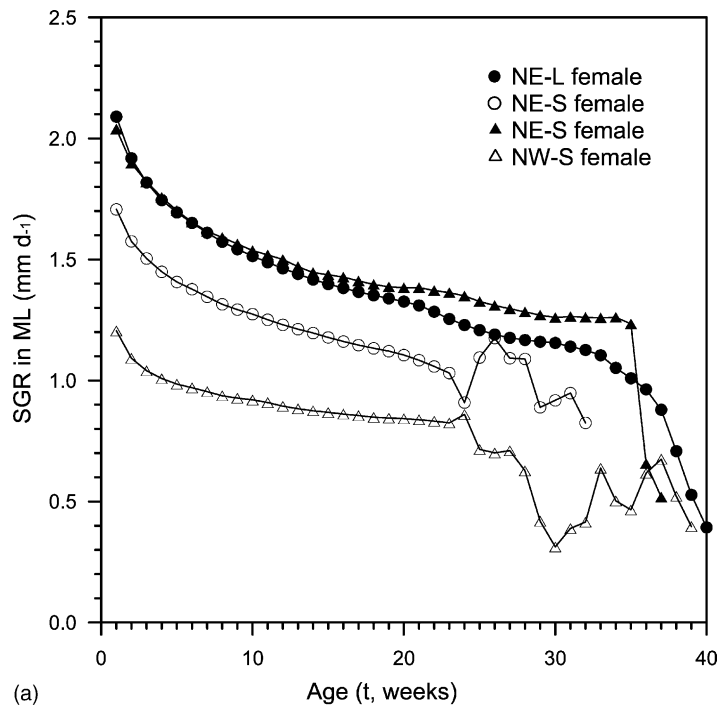


Fig. 8. SGR in ML of *O. bartramii* in the North Pacific: (a) female; (b) male.

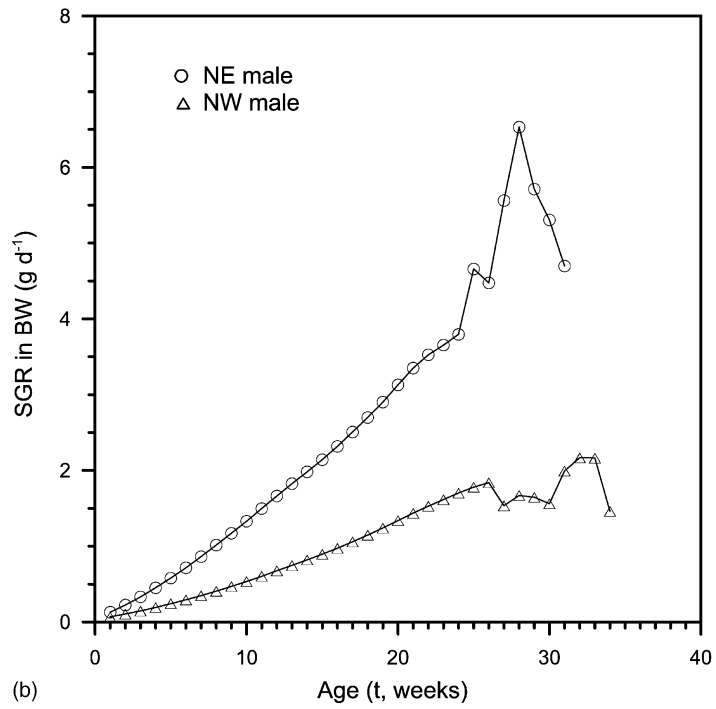
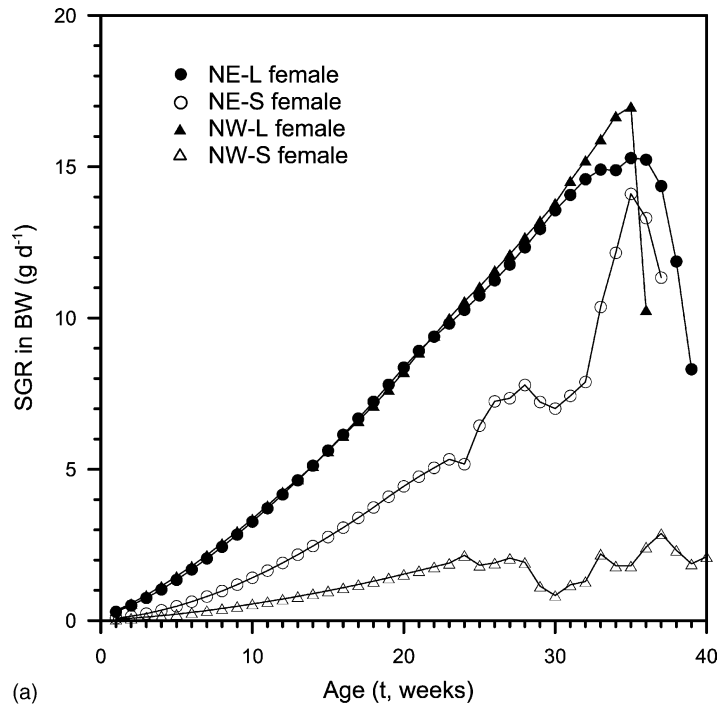


Fig. 9. SGR in BW of *O. bartramii* in the North Pacific: (a) female; (b) male.

is composed of two geographically separated populations possessing distinctive demographic characteristics (Figs. 4 and 5).

In addition to geographic separation, size composition (ML and BW) changed seasonally was also observed within each population. We proposed that distinctive size groups are due to a prolonged spawning season in terms of seasonal cohorts; those large female (LL) and non-LL ones (L, S, SS) of Murata (1990) could be autumn- and spring-breeding, respectively (Murakami et al., 1981; Murata, 1990). In this study we sampled large female animals (>350 mm ML), since there were no equivalent male animals available. This may indicate that the male population does not reach the same size. In the NE North Pacific, there are two size groups of females, corresponding to two seasonal cohorts, recruiting into the feeding ground in the Subarctic Frontal Zone during July–September (Fig. 11). Statolith microstructure analysis indicated that the hatching of large females (NE-L) peaked in October, and of small females (NE-S) peaked in December. The NE-L group coincides with an autumn cohort suggested by Yatsu et al. (1997), and the NE-S group is a winter cohort.

There are also two size groups of females recruited to the Subarctic Frontal Zone for feeding during July–September in the NW North Pacific. Small females (NW-S) are estimated primarily hatched in November and hatching extends to February, which is comparable to the winter–spring cohort suggested by Yatsu et al. (1997). Small females are also found geographically distinct from the large females (NW-L), which are distributed further north and are not accessible by the NW-S group. We found that linear ML to Ra relationship exhibited no geographic difference in large females (>350 mm ML) in contrast to significant difference between NE and NW geographic groups in both small females (<350 mm ML) and males (Fig. 5), and similar demographic characteristics of NW-L to NE-L (SGR, Figs. 8 and 9) lend us a supposition that NW-L and NE-L females may originate from a common population.

An apparent unbalanced sex ratio of the neon flying squids was found in this study, with male deficiency especially pronounced in the NE Pacific samples (Table 1). The hatching of NE males peaked in December, while that of NW males peaked in November. Yatsu et al. (1998) reported that male squid was rare

in the NE Pacific. Only 43 male specimens were caught in our chartered boat survey during the period of 5 July–17 August 1997; all were collected from the southern localities in late July and August (Fig. 1). Size and sex segregated migration may have evolved in some squid species in order to minimize cannibalism (Boyle and Boletzky, 1996). For *O. bartramii*, extended survey is needed to clarify the structure of the male population.

4.2. Growth and hatching time

The Gompertz function describes an exponential growth of organism with rapid decreasing rate, especially at early stages of fish larvae (Palomera et al., 1989). The neon flying squid populations of NE-L and NW-S females have shown this growth pattern; NE-L with larger initial ML ($L_0 = 40.20$) and lower decreasing rate ($g = 0.06$) (Fig. 6b) compared to those of NW-S ($L_0 = 22.02$, $g = 0.07$; Fig. 6a) (Table 2). In contrast, NE-S and NW-L females have grown as a power function indicating an unlimited growth pattern to adult stage; NW-L with larger initial ML ($a = 20.03$) and faster growth ($b = 0.82$) compared to NE-S ($a = 17.96$, $b = 0.79$). Decreased growth rates found in NE-L and NW-S females may function to reallocate energy for maturity, which is a recognized strategy in cephalopods (Wells and Clarke, 1996). We found seven mature females in the NE samples, contributing 2% to the total, and only juvenile/subadult stage (B: maturity stage) of females in the NW samples.

The exact time and locality of *O. bartramii* spawning is still required for fisheries management, although it has been postulated that it occurs in the subtropical North Pacific. Based on the specimen of paralarvae and mature female, several spawning localities have been suggested: southeastern waters of Honshu, Japan, in January–May (Okutani, 1968); around 25–26°N, 143–161°E in May for NW population, and 25–27°N, 170–164°W in April–May for NE population (Hayase, 1995); and subtropical waters close to Hawaiian Archipelago (Young and Hirota, 1990; Bower, 1996). Putting all available information together, we tentatively inferred that the hatching localities for *O. bartramii* to be in the waters approximately centered at 25°N, 155°W and 25°N, 145°E, respectively, for the NE and NW populations (Fig. 1). From GlobalSST image data set, we found that

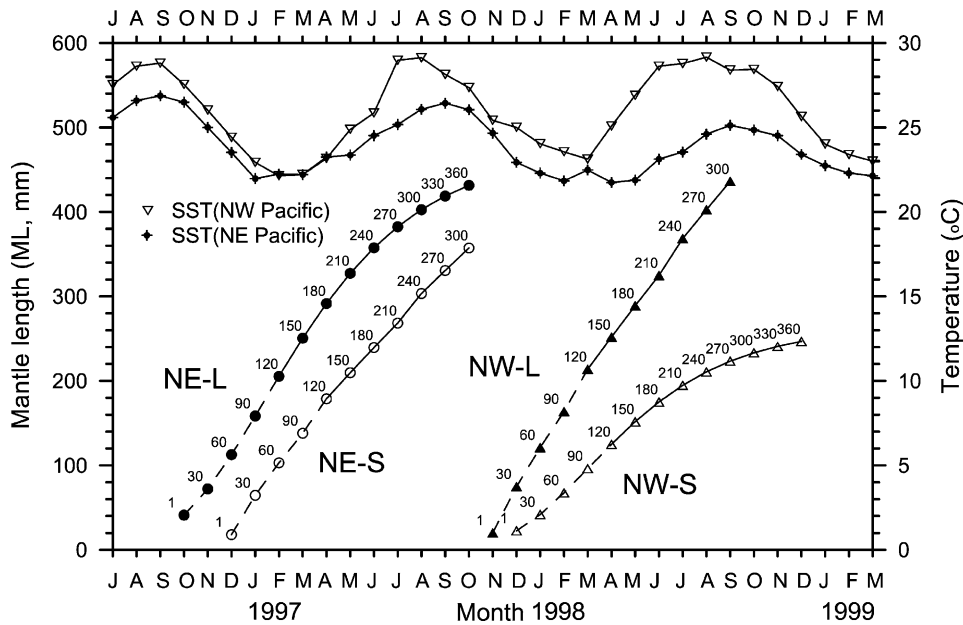


Fig. 10. Growth patterns of female *O. bartramii* cohorts (dashed line, paralarvae/juvenile stages; straight line, subadult/adult stages), and SST ($^{\circ}\text{C}$) in estimated hatching site in the North Pacific (open square, NW SST, filled square, NE SST).

monthly SST ($^{\circ}\text{C}$) between mid-1996 to early 1999 in the hatching areas, fell within the range of 21.7–26.9 and 22.1–29.2 $^{\circ}\text{C}$, for the NE and NW North Pacific, respectively (Fig. 10). Seasonal changes of SST are similar between NE and NW regions but NW is always apparently higher than NE. Relatively small temperature changes could have dramatic impact on cephalopod growth as shown by captive *Loligo forbesi* (Forsythe, 1993). The hypothetical sensitive effects have been shown by studies based on statolith microstructure analysis; squids which were hatched in warmer waters had higher growth rate in later development stages and reached larger adult size (*Illex illecebrosus*: Dawe and Beck, 1997; *Lolliguncula brevis*: Jackson et al., 1997; *Loligo pealei*: Hatfield et al., 2001). Averaged growth trajectories of two geographic populations and two cohorts of *O. bartramii* were shown together with the SST of the hatching area (Fig. 10). We select two extreme groups, of NE-L (rapid) and NW-S (slow), both with Gompertz type growth, for comparison. The October-spawn NE-L female (autumn cohort) encountered a decreasing temperature regime of 26.5–23.5 $^{\circ}\text{C}$ during paralarva/juvenile stage of less than 90 days, while that of

December-spawn NW-S female (winter cohort) met a regime of 25.0–23.5 $^{\circ}\text{C}$. Higher ambient temperature for NE-L females at early life stage might have caused its faster growth to reach a larger adult size (ca. 400 vs. 200 mm ML at 49 weeks; Fig. 6a and b). The growth of NW-L and NE-L females is similar before 30 weeks with 350 mm ML (Fig. 6a and b). The growth trajectory of NW-L and NE-L females, which is better depicted by a power function and a Gompertz function, respectively, could be a result of calculation from younger and older populations. However, when we estimated the growth function of NE-L female with equivalent data set of squids aged less than 43 weeks, the power curve fitted best. That is, when the squid is under an unlimited growth of juvenile/subadult stage, the power function can describe growth trajectory well, while the squid is under a limited growth of adult stage, the Gompertz function can be better.

4.3. Migration patterns

Different migratory routes of *O. bartramii* are shown by spring- and autumn-breeding cohorts (Fig. 15 of Murata and Hayase, 1993), as evidenced

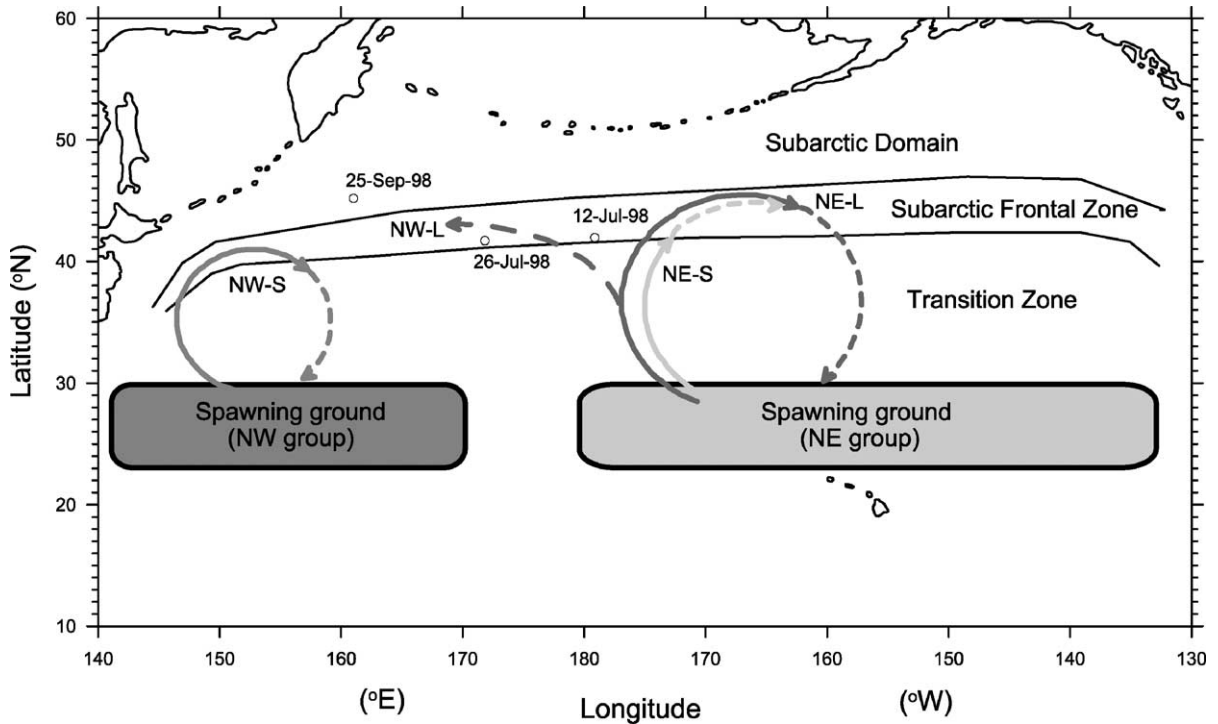


Fig. 11. Schematic diagram showing a possible migration pattern of *O. bartramii* in the North Pacific.

by only large females (>340 mm ML, autumn cohort) present in the Subarctic Domain in contrast to juveniles (150–250 mm ML; male and female) in the Transition Zone (Kubodera et al., 1983). Based on the growth patterns found in this study and tempo-spatial catch distribution (Anon., 1996–2001), a possible major migratory pattern of *O. bartramii* in the North Pacific is modified to that proposed by Murata and Hayase (1993) (Fig. 11). The NW-S female and male squids migrate a short route as described in previous studies, because they encounter lower temperature at their earlier life (aged ca. 330 days, when temperature dropped to 27.4°C in November, Fig. 10). Longer migratory routes are exhibited by large females: the NE-L group hatched in September–October (autumn cohort of NE; Fig. 3), and reached its maximal size of about 420 mm ML in 360 days (Fig. 10). The migration of NW-L females has not been suggested by Murata and Hayase (1993) because of rare data from NW North Pacific. It can be inferred from our samples, that NW-L females possibly originate from a part of the NE-L population that hatched in

November–January, then migrate westerly to relatively warmer NW region during winter and continued to grow exponentially (Figs. 6a and 10). They reached the NW Pacific in the Subarctic Frontal Zone at about 30 weeks with 350 mm ML, represented by samples of 12 and 26 July and 25 September (Figs. 6a and 11 and Table 1). No between-group difference is shown by NE-L and NW-L females of <350 mm ML (Fig. 6a and b). Also, no distinctive relationships of Ra to In (Fig. 4) and ML to Ra (Fig. 5) between geographic groups are concluded statistically; by which parameters we summarized into a dendrogram resulted from a cluster analysis measured by normalized Euclidean distances (Fig. 12). The similarity of NW-L to NE-L is explainable because they experienced the same NE environment before subadult stage of ca. 30 weeks and both growth trajectories could be described best by a power function when data sets of equivalent period were calculated. Currently, neither spawning populations of *O. bartramii* are confirmed, nor are high concentrations of their larvae found. However, our backward calculation based on statolith

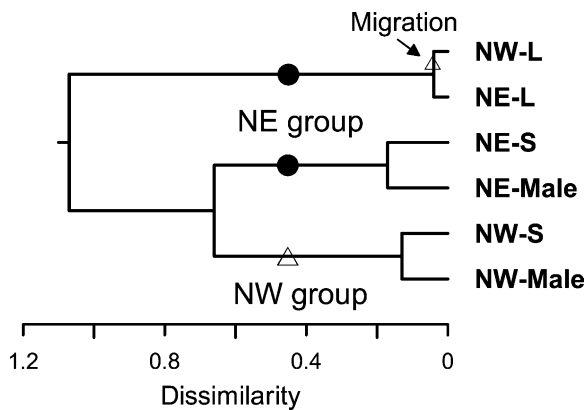


Fig. 12. Similarity of the geographic groups of *O. bartramii* cohorts in the North Pacific, based on growth parameters.

microstructure analysis demonstrates an effective substitute that provides some basic demographic information for management propose.

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