Stage-specific vertical distribution of Alaska plaice (*Pleuronectes quadrituberculatus*) eggs in the eastern Bering Sea

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Abstract—The stage-specific distribution of Alaska plaice (*Pleuronectes quadrituberculatus*) eggs in the southeastern Bering Sea was examined with collections made in mid-May in 2002, 2003, 2005, and 2006. Eggs in the early stages of development were found primarily offshore of the 40-m isobath. Eggs in the middle and late stages of development were found inshore and offshore of the 40-m isobath. There was some evidence that early-stage eggs occur deeper in the water column than late-stage eggs, although year-to-year variability in that trend was observed. Most eggs were in the later stages of development; therefore the majority of spawning is estimated to have occurred a few weeks before collection—probably April—and may be highly synchronized among local spawning areas. Results indicate that sampling with continuous underway fish egg collectors (CUFES) should be supplemented with sampling of the entire water column to ensure adequate samples of all egg stages of Alaska plaice. Data presented offer new information on the stage-dependent horizontal and vertical distribution of Alaska plaice eggs in the Bering Sea and provide further evidence that the early life history stages of this species are vulnerable to near-surface variations in hydrographical conditions and climate forcing.

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Knowledge of the vertical distributions of fish eggs and larvae is important to understanding how wind and currents may affect early life stages. The eggs of several pleuronectid species in the North Pacific are positively buoyant (Pearcy, 1962; Bailey et al., 2005). Retention of pelagic eggs at the top of the water column exposes them to wind mixing that ensures an adequate oxygen supply for the developing egg, but also increases susceptibility of the eggs to stochastic wind events and adverse advection. Consistent baroclinic flows below the wind-mixed layer facilitate retention of developing eggs, but also could expose eggs to anoxia and increased predation. Vertical position often changes with development, and stage-dependent ascension can occur slowly throughout the developmental period, or quickly once eggs reach a critical stage.

Alaska plaice (*Pleuronectes quadrituberculatus*) is one of the major shallow water flatfishes in the Bering Sea; however, there is not a significant fishery for the species. Alaska plaice are primarily harvested as bycatch in fisheries targeting other, more lucrative groundfishes, and a large portion of the Alaska plaice biomass is discarded. Adult Alaska plaice spawn in spring over the middle Bering Sea shelf at depths of 50–100 m, and egg and larval stages are pelagic (Bailey et al., 2003). Previous work (Duffy-Anderson et al., 2010) has shown that Alaska plaice larvae occur in the upper 20 m of the water column, but vertical patterns of egg distribution have not been determined.

The continuous underway fish egg sampler (CUFES; Checkley et al., 1997) is a tested collection system used in sampling near-surface eggs from a fixed depth (3 m) and has the advantage of being able to sample eggs in adverse weather conditions when tows with nets are not possible (Checkley et al., 2000; Lo et al., 2001). The CUFES has been used in other regions to sample and estimate the densities of marine fish eggs in the water column (Dopolo et al., 2005; Pepin et al., 2005). Accurate derivation of depth-integrated egg densities from near-surface estimates requires a complete understanding of patterns of vertical egg distribution with depth and development, but this information is not available for a number of fish species in the Bering Sea, including Alaska plaice.

The goals of the present study were 1) to determine the developmental stage of Alaska plaice eggs collected from depth-discrete tows conducted in the eastern Bering Sea; 2) to examine the vertical distribution of staged eggs; and 3) to determine whether the CUFES could be a suitable sampler of Alaska plaice eggs in the Bering Sea.

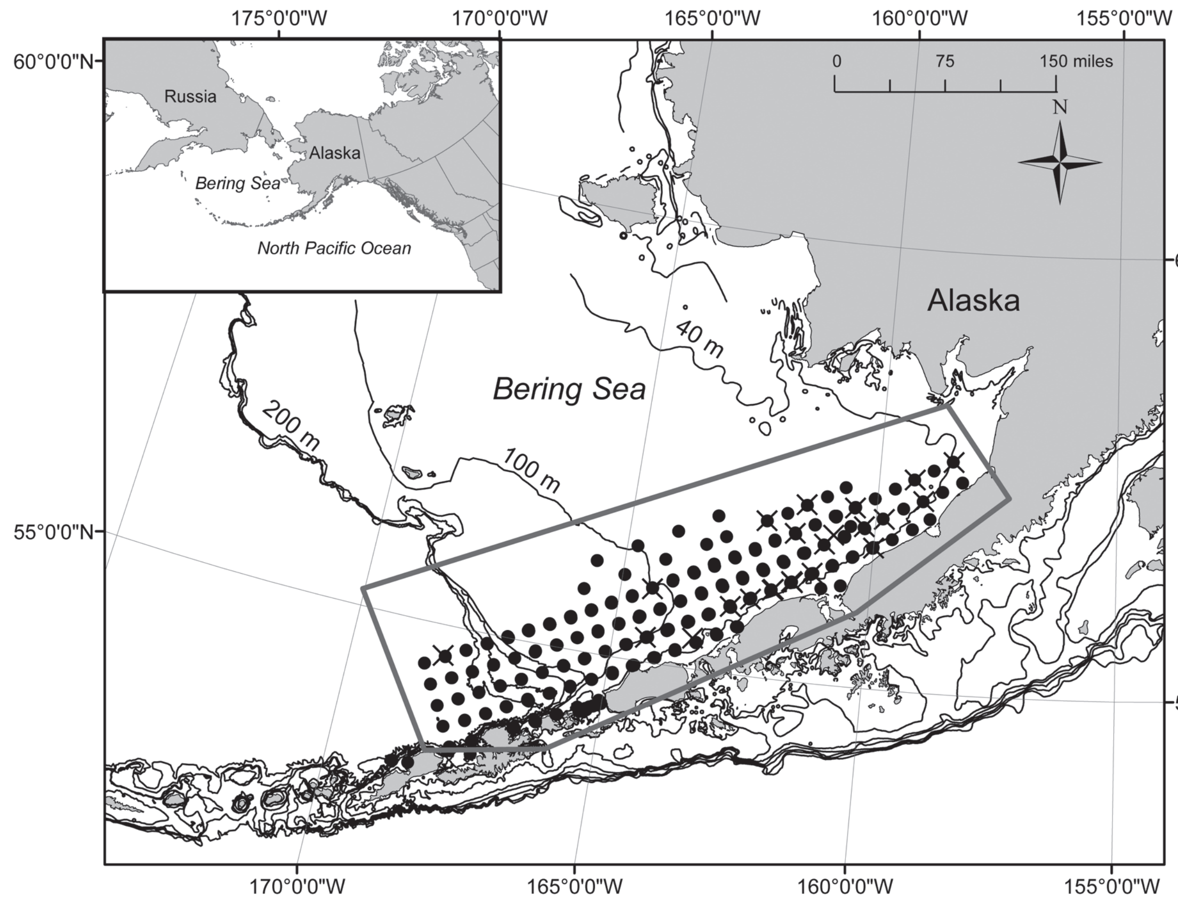

Figure 1

Map of study region (inset) and stations where eggs of Alaska plaice (*Pleuronectes quadrituberculatus*) were collected with the multiple opening and closing net and environmental sampling system (✕) and neuston net (●) tows in the eastern Bering Sea during 2002–06. The polygon delineates the sampling area.

Materials and methods

Alaska plaice eggs were obtained from a series of fisheries research cruises conducted by the Alaska Fisheries Science Center (AFSC) along the Alaska Peninsula in the eastern Bering Sea in 2002, 2003, 2005, and 2006 (Fig. 1, Table 1). Eggs were collected from surface waters (<0.5 m depth) with a Sameoto neuston net with 505-µm mesh (Sameoto and Jaroszynski, 1969; Jump et al., 2008). Depth-discrete sampling was conducted by using a 1-m^2 multiple opening and closing net and environmental sampling system (MOCNESS; Wiebe et al., 1976) with 505-µm mesh nets in 2003 and 2005. Depth intervals sampled were 0–10 m, 10–20 m, 20–30 m, 30–40 m, 40–50 m, and >60 m. Oceanographic variables were collected simultaneously with all sampling, and these data have been published elsewhere (Duffy-Anderson et al., 2010).

All eggs were fixed in 5% formalin, sorted, identified, and enumerated at the Plankton Sorting and Identification Center in Szczecin, Poland. Egg identifications were verified, and Alaska plaice eggs were measured and staged at the Alaska Fisheries Science Center in Seattle, WA.

Table 1

Number of Alaska plaice (*Pleuronectes quadrituberculatus*) eggs collected and staged by year and gear type. MOCNESS=multiple opening and closing net and environmental sampling system.

Year	Cruise dates	Gears used	Number of eggs collected and staged
2002	12–21 May	Neuston net	16
		MOCNESS	2
2003	17–24 May	Neuston net	26
		MOCNESS	353
2005	10–20 May	Neuston net	295
		MOCNESS	867
2006	8–19 May	Neuston net	615

Developmental stages of eggs

Stages of Alaska plaice eggs were determined according to developmental criteria standardized and described by Blood et al. (1994) for walleye pollock (*Theragra chalcogramma*). Staging criteria for walleye pollock are the standard criteria used to determine northern marine teleost egg development and were easily adapted to egg development in Alaska plaice. Modifications were made to the protocol in order to accommodate additional embryonic growth in Alaska plaice. For the present study, the last stage (21) in the egg development schedule for walleye pollock is defined as that stage when the tail tip reaches the back of the embryo's head and two stages are added: stage 22, when the tail tip extends to ¼ of the circumference of the egg beyond the snout; and stage 23, when the tail tip extends to ½ of the circumference of the egg beyond the snout.

Eggs were then binned into three broader categories that comprised 1) early-stage eggs (E: stages 1–12), which includes all stages before the closing of the blastopore; 2) middle-stage eggs (M: stages 13–15), when the blastopore is closed, the margin of the tail is defined, and the tail bud is thick, but the margin remains attached to the yolk; and 3) late-stage eggs (L: 16–23), when the tail lifts away from yolk and lengthens and encircles the top half of the yolk to extend just beyond the head of the embryo. The late-stage period was further subdivided into three stages after determining that the majority of eggs were in one of the following stages of development; early-late stage (EL: stages 16–18); middle-late stage (ML: 19–21); and late-late stage (LL: 22–23).

Collections with the neuston net

Eggs were collected from surface waters (<1 m depth) across the southern Bering Sea shelf in the vicinity of the Alaska Peninsula. Collections were made over the basin, outer, middle, and inner shelves. Eggs from each tow were staged and the hypothesis that there were differences in geographic (horizontal) distribution with stage of development was examined by using Cramer-von Mises tests.

Vertical distributions of eggs determined with MOCNESS tows

The hypothesis that vertical patterns in egg abundance vary with depth and developmental stage was evaluated by using data collected from MOCNESS tows. A fourth root transformation was used to improve the normality of the data. In 2003, a series of MOCNESS tows were conducted at a single station, whereas in 2005, MOCNESS tows were conducted at multiple stations over the Bering Sea shelf. A general linear model ANOVA was used for each cruise by using haul as a blocking factor in 2003, and station as a blocking factor in 2005. If significant differences with depth were found, the analysis was followed with Fisher's least significant difference comparisons (Milliken and Johnson, 1992). We also checked for autocorrelation in 2003 (Durbin Watson statistic) because in that year samples were taken over time at a single station.

Results

Stages of developing eggs

More than 2100 eggs were examined for this work (Table 1), of which more than 950 eggs were collected from neuston nets and the remainder from MOCNESS tows. The earliest developmental stage observed was stage 5 (32 cells) (Table 2); we estimated these eggs would be about 1 day old at *in situ* temperatures (4°C). Egg development studies of walleye pollock and arrowtooth flounder (*Atheresthes stomias*) have established that the time required to reach stage 5 is 18–28 hours at about 3°C (Blood, 2002; Blood et al., 2007), and we assumed similar rates for Alaska plaice eggs. The presence of stage-5 eggs indicates that residual spawning occurred in mid-May; however, the vast majority of the eggs were late-stage eggs (Table 2), indicating that most spawning occurred a few weeks before sampling (Pertseva-Ostroumova, 1961). Most eggs collected were at stage 22. Hatching occurs at stage 23; the eyes of embryos are fully pigmented and numbers of eggs are greatly reduced in contrast to stage 22.

Collections with the neuston net

Eggs collected from neustonic surface collections represented all stages of development (Fig. 2). Results of all pairwise Cramer-von Mises tests for differences in spatial distributions showed that there were no significant differences between the geographic distributions of any stages of larvae, except between the geographic distributions of EL and ML ($P=0.002$). However, there were some trends that could be discerned. Earliest stage eggs collected in the neuston layer appeared to concentrate offshore of the 40-m isobath, over bottom depths ranging from 40 to 75 m. Eggs in middle stages of development appeared to spread shoreward toward shallower depths, but catches of eggs in both the early and middle stages of development were comparatively low. Late-stage eggs occurred over depths ranging from 40 to 100 m.

Vertical distributions of eggs determined with MOCNESS tows

Vertical distributions of Alaska plaice eggs showed differences in depth distribution with ontogenetic stage (Fig. 3), and differences between years. In 2003, there was no significant effect of haul and therefore no autocorrelation (Durbin Watson statistic=1.91; effect of haul), and eggs were generally distributed throughout the water column. There was only one egg collected in the early stage and it was located in the deepest depth stratum (40–50 m). There were no collections of eggs

Table 2

Results of staging Alaska plaice (*Pleuronectes quadrituberculatus)* eggs and the percentage of eggs in each developmental stage bin by gear type (early: stages 1–12; middle: stages 13–15; late: stages 16–23). The late stage was subdivided into three categories (early late: stages 16–18; middle late: stages 19–21; and late late: stages 22–23). Stages were adapted from Blood et al. (1994) and two developmental stages were added for this study. MOCNESS=multiple opening and closing net and environmental sampling system.

	Developmental stage	Number of eggs/stage (neuston net and MOCNESS)	Percentage of total eggs/stage (neuston net and MOCNESS)		Neuston net (percentage of eggs collected)	MOCNESS (percentage of eggs collected)
Early	1	0	0			
	2	0	0			
	3	0	0			
	4	0	0			
	5	3	0.14			
	6	7	0.32			
	7	20	0.92			
	8	2	0.09			
	9	20	0.92			
	10	7	0.32			
	11	14	0.64			
	12	10	0.46			
				Total	8.1	0.5
Middle	13	10	0.46			
	14	23	1.06			
	15	51	2.35			
				Total	8.4	0.4
Early late	16	58	2.67			
	17	158	7.27			
	18	67	3.08			
				Total	23.0	5.2
Middle late	19	209	9.61			
	20	230	10.58			
	21	285	13.11			
				Total	30.2	35.7
Late late	22	727	33.44			
	23	272	12.51			
				Total	30.3	58.2

in the middle stages of development (stages 13–15). Among late-stage eggs in 2003, the densities of egg abundances were depressed in the near surface waters (0–10 m) and significantly so for ML and LL stages (Table 3). In general however, most eggs were collected from above the mixed layer (<30 m). In 2005, a different pattern emerged; late-stage eggs consistently occurred at shallower depths than did earlier stages (Fig. 3), and the majority were collected in near-surface waters. Statistical examination revealed that more eggs were collected from depths 0–10 m and 10–20 m than in any of the deeper depths.

Considered collectively, approximately 34% of the catch in the two years occurred in the top 10 m of the water column, 24% occurred between 10 and 20 m, 18% between 20 and 30 m, 11% between 30 and 40 m, 8% between 40 and 50 m, and 5% between 50 and 60 m depth.

Discussion

This is the first study to describe stage-dependent vertical and horizontal distribution of Alaska plaice eggs. Our data indicate that spawning occurs offshore of the 40-m isobath, and likely near-bottom, confirming hypotheses outlined in Bailey et al. (2003). Eggs occur throughout the water column, but many eggs occur in the upper water column (<30 m depth). The vast majority of eggs collected in the present study were in the later stages of development, and we estimate that the majority of spawning occurred a few weeks before collection. Maxi-

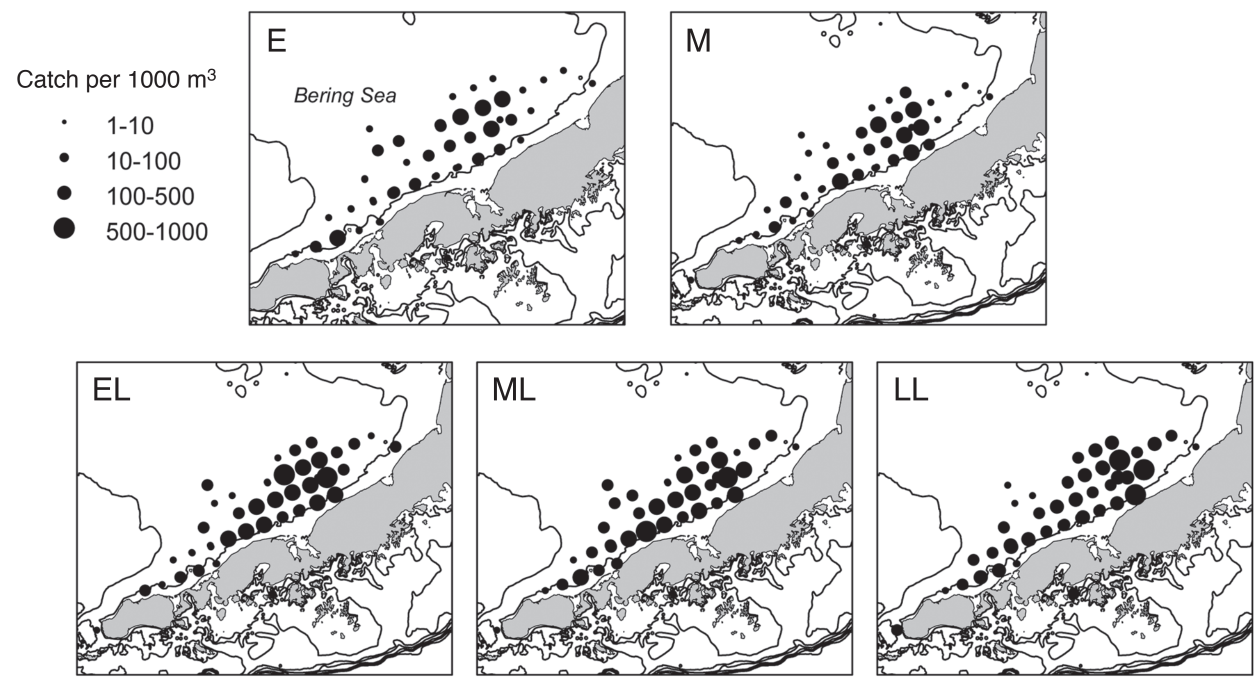

Figure 2

Abundance and geographic distribution of Alaska plaice (*Pleuronectes quadrituberculatus*) eggs (at different stages: early [E] and middle [M]; and at three stages within the late stage: early late [EL], middle late [ML], late late [LL]) collected in the neuston layer over the middle Bering Sea shelf. Catch is expressed as eggs/1000 m^3. The period of early-stage (E) eggs comprises stages 1–12, the period of middle-stage (M) eggs comprises stages 13–15, and the period of late-stage (L) eggs comprises stages 16–23.

mum larval abundance in the Bering Sea occurs in May (Duffy-Anderson et al., 2010) and probably reflects peak hatching of eggs spawned in April and a relatively high degree of spawning synchrony.

The geographic sampling area over which these eggs were collected was small compared to the potential spawning area over the Bering Sea continental shelf, and available evidence indicates that Alaska plaice do spawn over a large portion of the middle domain of the continental shelf (Zhang et al., 1998). The wind-mixed layer in the Bering Sea generally extends to 25–30 m in spring (Stabeno et al., 2001), and our data reveal that Alaska plaice eggs primarily occur above or within this layer. As such, the eggs are vulnerable to the stochastic effects of wind activity, which could disperse them widely over the shelf, especially in early spring months (March–April) when the likelihood of storm events is high. However, prevailing winds over the shelf in late spring–summer are southwesterly and would therefore transport late-stage eggs and newly hatched larvae from the middle shelf toward nursery areas along the Alaska mainland coast. Indeed, previous work has shown that Alaska plaice larvae are relatively rare over the continental shelf (Bailey et al., 2003), lending credence to the idea of shoreward transport of older egg stages and hatched larvae. It should be noted that retention in near-surface layers is also likely to promote faster rates of egg development because temperatures in the upper water column are 1–3°C warmer than those at depth over the middle shelf during spring.

Alaska plaice eggs do occur in near-surface waters, making them accessible to CUFES system, but many eggs also occur below the depths sampled with the CUFES. Therefore, abundance determined from eggs caught with the CUFES system may be underestimated—particularly the abundance of early stages that might be deeper in the water column. This observation has been made elsewhere (Lo et al., 2001; Dopolo et al., 2005), and at least in the case of Alaska plaice, we recommend that sampling with the CUFES system be supplemented with sampling of the entire water column to ensure adequate sampling of eggs at all stages of development. Moreover, sampling earlier in the spring, in March–April, for earlier stages is encouraged.

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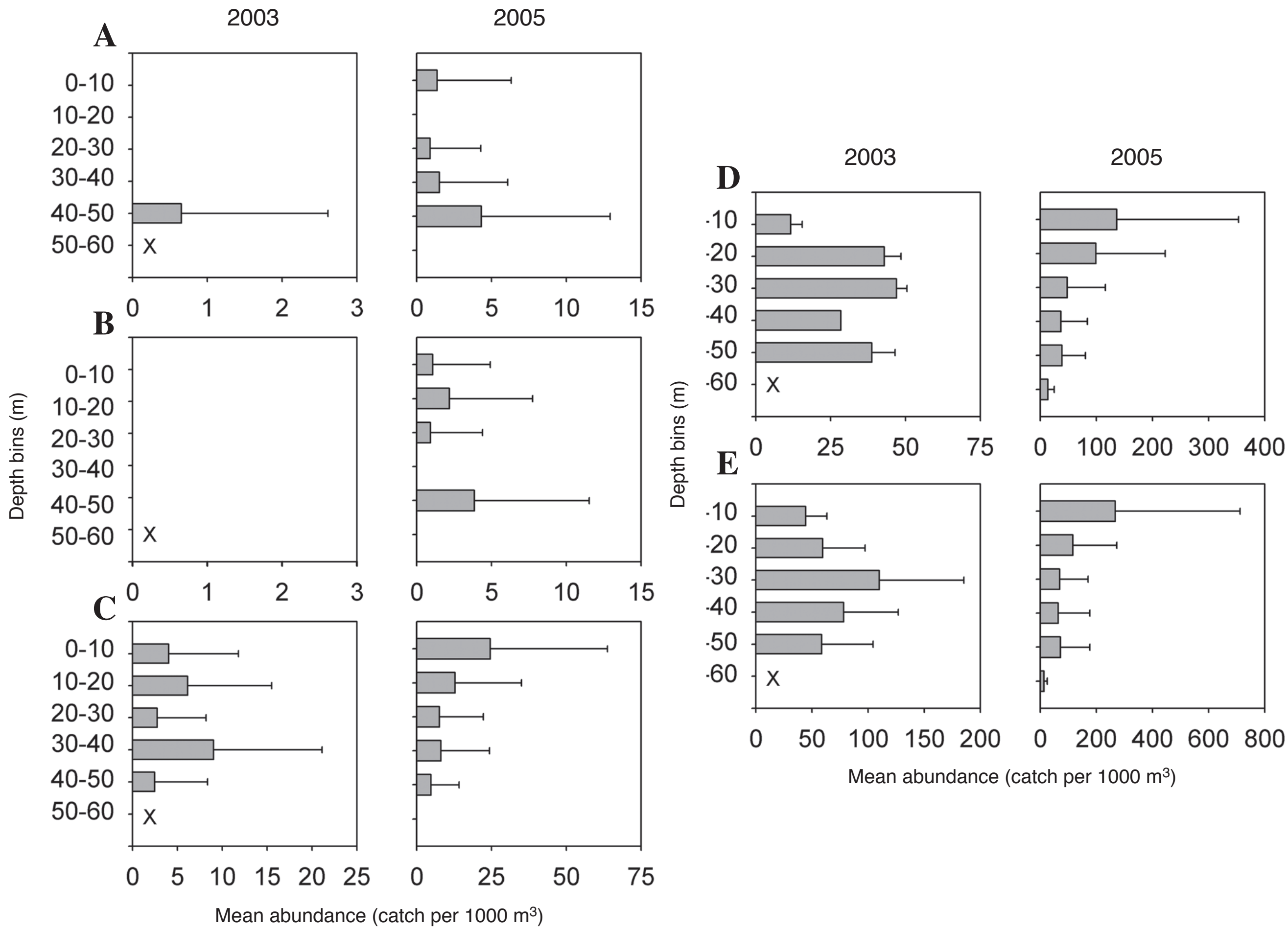

Figure 3

Mean abundance (± standard deviation) of Alaska plaice (*Pleuronectes quadrituberculatus*) eggs by developmental stage and depth. The symbol × indicates that no sample was taken at that depth. Data are derived from catches with the multiple opening and closing net and environmental sampling system in 2003 and 2005. (**A**) Early stage, (**B**) middle stage, (**C**) early-late stage, (**D**) middle-late stage, (**E**) late-late stage.

Table 3

Statistical comparisons Off differences in abundances of Alaska plaice (*Pleuronectes quadrituberculatus*) eggs in 2003 and 2005 by depth bin. Significance is noted at $P<0.05$. ns=not significant. ML=middle late stage. LL=late late stage.

ML 2003	0–10 m	10–20 m	20–30 m	30–40 m	40–50 m	50–60 m	60+ m
0–10 m	ns						
10–20 m	0.004	ns					
20–30 m	<0.001	ns	ns				
30–40 m	0.035	ns	ns	ns			
40–50 m	0.001	ns	ns	ns	ns		
50–60 m	ns	ns	ns	ns	ns	ns	
60+ m	ns	ns	ns	ns	ns	ns	ns

continued

Table 3 (continued)

LL 2003	0–10 m	10–20 m	20–30 m	30–40 m	40–50 m	50–60 m	60+ m
0–10 m	ns						
10–20 m	ns	ns					
20–30 m	0.002	0.017	ns				
30–40 m	ns	ns	ns	ns			
40–50 m	0.041	ns	ns	ns	ns		
50–60 m	ns	ns	ns	ns	ns	ns	
60+ m	ns	ns	ns	ns	ns	ns	ns
ML 2005	**0–10 m**	**10–20 m**	**20–30 m**	**30–40 m**	**40–50 m**	**50–60 m**	**60+ m**
0–10 m	ns						
10–20 m	ns	ns					
20–30 m	ns	0.009	ns				
30–40 m	ns	0.017	ns	ns			
40–50 m	0.005	0.001	ns	ns	ns		
50–60 m	ns	0.022	ns	ns	ns	ns	
60+ m	ns	0.032	ns	ns	ns	ns	ns
LL 2005	**0–10 m**	**10–20 m**	**20–30 m**	**30–40 m**	**40–50 m**	**50–60 m**	**60+ m**
0–10 m	ns						
10–20 m	ns	ns					
20–30 m	0.013	ns	ns				
30–40 m	0.003	0.022	ns	ns			
40–50 m	<0.001	<0.001	0.017	ns	ns		
50–60 m	ns	ns	ns	ns	ns	ns	
60+ m	.007	0.03	ns	ns	ns	ns	ns

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