Body size dependence of euphausiid spatial patchiness

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Abstract

We analyzed size-dependent variations in spatial patchiness of the eight numerically dominant euphausiid species in the California Current System (*Euphausia pacifica*, *Nematoscelis difficilis*, *Nyctiphanes simplex*, *Thysanoessa gregaria*, *Euphausia recurva*, *Euphausia gibboides*, *Thysanoessa spinifera*, and *Euphausia eximia*). Patchiness was measured by using a count-based statistic using euphausiid densities and applied to 11 yr of detailed size-specific enumerations from the California Cooperative Oceanic Fisheries Investigations program. We rejected the hypothesis of size-independent patchiness for seven of the eight species. The most common pattern observed was a "U-shaped" curve, showing elevated patchiness in the smallest size classes, a rapid decrease in patchiness of intermediate-sized euphausiids, and a later increase in patchiness of adults following the onset of reproductive maturity. These size-dependent changes parallel ontogenetic changes in spatial dispersion observed for some marine fishes. The initial descending limb of the patchiness curve appears to be caused by turbulent diffusion, while the later ascending limb of the curve is consistent with the onset of predator-induced aggregation behavior. The patterns were surprisingly consistent across years and different reproductive characteristics (egg-brooding vs. broadcast spawning euphausiids).

The ecological and evolutionary importance of spatial pattern of marine organisms has long been recognized (Hutchinson 1953; Steele 1978; Levin 1992), and efforts to establish and understand spatial distributions are a central issue in marine ecology. Patchiness (its existence, causes, dynamics) has been investigated for numerous organisms ranging from phytoplankton (Kierstead and Slobodkin 1953; Wroblewski and O'Brien 1976) to fish (Hewitt 1981) and on different spatial scales (Weber et al. 1986; Steele and Henderson 1992; Levin et al. 1993). Factors leading to aggregation are varied, with physical and biological processes contributing differentially to species' distributions. Wroblewski and O'Brien (1976) found that the combination of both physical factors (nutrients, light, and other factors) and grazing pressure ultimately determine the critical size as well as persistence of a phytoplankton patch. Weber et al. (1986) described the variance in the spatial spectra for temperature, phytoplankton and Antarctic krill. Physical processes were largely responsible for the red spectrum displayed by phytoplankton, but in order to explain the flatter spatial spectrum of krill, biological processes were invoked (e.g., swimming behavior and/or vertical migration).

Common marine planktivores, such as adult pelagic fish, have distributions that are extremely patchy, typically caused by their schooling behavior (Matsuura and Hewitt 1995). Schooling may help fishes avoid predators, increase efficiency of finding and exploiting prey patches, increase swimming efficiency, and ensure reproduction (Matsuura and Hewitt 1995; Parrish and Turchin 1997). Previous studies of variations of patchiness with body size of some pelagic fishes have reported a "U-shaped" curve with ontogeny (Hewitt 1981; McGurk 1987; Matsuura and Hewitt 1995). In this pattern, patchiness of eggs and young

larvae is typically very high, reflecting the aggregation of the spawning adults, followed by a rapid decrease in patchiness of older larvae as a consequence of turbulent diffusion. Later in the life history, patchiness increases rapidly as fish develop better sensory capabilities and body musculature, leading to the onset of schooling behavior (Hewitt 1981; Matsuura and Hewitt 1995). Fish patchiness may also be related to fish spawning modes and/or habitats (McGurk 1987). The distributions of demersal vs. pelagic eggs are affected differently by turbulent diffusion. Demersal spawning species are not affected by diffusion until the larval stages emerge into the water column, in contrast to free-spawning pelagic species whose propagules experience turbulence from the moment of spawning. These differences are thought to contribute to the different magnitudes of the U-shaped pattern observed in anchovy and jack mackerel, which are pelagic spawners, in contrast to Pacific herring, a demersal spawner (Hart 1973). The processes creating aggregated distributions are therefore of both physical and biological origin. The relative contribution of the two, however, is highly variable among species as a consequence of the variability of species characteristics such as body size, swimming ability, spawning mode, and other life history traits.

Euphausiids are relatively large crustacean members of the zooplankton or micronekton. Many species have been reported to form dense aggregations, and in general their distributions are known to be extremely patchy, especially as adults (Mauchline 1980). When mature, euphausiids bear five pairs of pleopods that confer excellent routine swimming ability, in addition to their rapid caridoid escape behavior made possible by a muscular abdomen (Mauchline 1980). Hence, as adults, euphausiids have the potential to exhibit behavioral control over their local distributions.

Here we investigate patchiness as a function of euphausiid body size. We were specifically motivated to
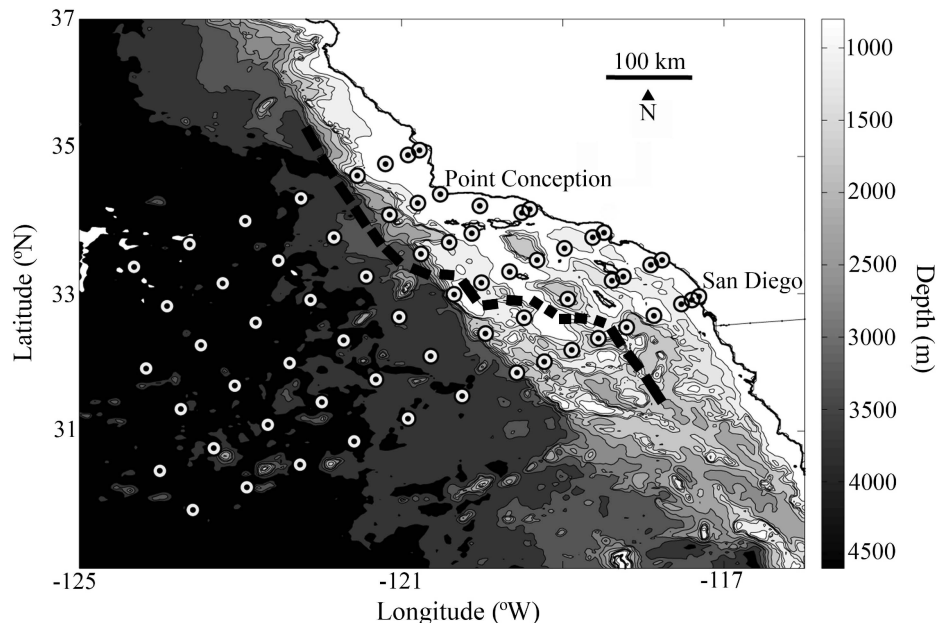
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Fig. 1. Sampling stations considered in our analysis, from the southern portion of the CalCOFI grid. Dashed line marks the separation between the "inshore" and "offshore" region. Gray shading indicates bottom topography (depth, in meters).

determine whether the U-shaped pattern documented for marine fishes is applicable to euphausiid crustaceans. In addition to testing the null hypothesis of size-independent spatial patchiness of euphausiids, we sought to determine whether patchiness varies with reproductive characteristics (free spawning vs. egg brooding) of different euphausiid species. For these analyses we utilize the extraordinary data from E. Brinton's career analyses of euphausiid population biology in the California Current System (Brinton and Townsend 2003).

Methods

Euphausiid collection—Euphausiids were sampled by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program. Time series of euphausiid abundance have been presented by Brinton and Townsend (2003). We restricted our analyses to the Southern California portion of the CalCOFI pattern (Fig. 1) since this was the region most consistently sampled over time. Only nighttime samples were considered as they more accurately represent the underlying abundances; many of the species considered here are known to either exhibit diel vertical migration, net avoidance, or both (Brinton 1967). Eleven years of data (1953–1959, 1969, 1978, 1984, and 1991) were used, from winter, spring, summer, and fall cruises in most years, except 1978, when we did not have data for the fall, and 1991, when only springtime data were available (Table 1). These 11 yr were selected because enumerations were available by euphausiid species and size class (to the nearest mm) from 1-mm-sized individuals to adults. The smallest size class considered here (1 mm) corresponds to the calyptopis phase. The water column was sampled by a 1-m ring net from 140 to 0 m in 1953–1959, the same net

from 210 to 0 m in 1969, and a 0.71-m-diameter bongo net sampled from 210 to 0 m from 1978 onward (Table 1); net mesh sizes were either 0.550 mm or 0.505 mm (details in Ohman and Smith 1995). Numbers of euphausiids per 1000 m³ of water filtered were converted to numbers m^{-2} from the following equation:

$$\frac{\text{No.}}{\text{m}^2} = \left[\frac{\left(\frac{\text{No.}}{1000 \text{ m}^3} \right)}{1000} \right] \text{Max Depth} \qquad (1)$$

where Max Depth is the maximum fishing depth of the sampling net.

The species considered here have different distributional ranges both in the Northeast Pacific and within the Southern California CalCOFI grid. While the eight species we analyze are the numerically dominant euphausiids in this region, they are neither restricted to our sampling area nor equally distributed within this portion of the grid. The following classification is from Brinton and Townsend (2003): cold water; widespread, oceanic, young phases commonly coastal: *Euphausia pacifica*; cold water, coastal; strong net avoider: *Thysanoessa spinifera*; transition zone—cool; animals widespread within thermocline, not vertical migrators: *Nematoscelis difficilis*, *Thysanoessa gregaria*; transition zone—warm; to west and southwest in survey sectors, vertical migrators: *Euphausia recurva* and *Euphausia gibboides*; and subtropical, and marginally tropical: *Euphausia eximia*, oceanic, and *Nyctiphanes simplex*, coastal.

The patchiness index—In order to quantify patchiness, we used an index modified from Lloyd's original index

Table 1. Years and seasons included in this study. Sampling protocol indicated for each year.

Year	Season	Net used	Depth sampled (m)	Mesh size (mm)
1953	Winter, spring, summer, fall	1-m ring net	140	0.550
1954	Winter, spring, summer, fall	1-m ring net	140	0.550
1955	Winter, spring, summer, fall	1-m ring net	140	0.550
1956	Winter, spring, summer, fall	1-m ring net	140	0.550
1957	Winter, spring, summer, fall	1-m ring net	140	0.550
1958	Winter, spring, summer, fall	1-m ring net	140	0.550
1959	Winter, spring, summer, fall	1-m ring net	140	0.550
1969	Winter, spring, summer, fall	1-m ring net	210	0.505
1978	Winter, spring, summer	0.71-m bongo net	210	0.505
1984	Winter, spring, summer, fall	0.71-m bongo net	210	0.505
1991	Spring	0.71-m bongo net	210	0.505

(Lloyd 1967). Lloyd's index, P, was designed for use with counts and is defined as follows:

$$P = 1 + \left(\frac{(\sigma^2 - m)}{m^2} \right) \qquad (2)$$

where m and σ^2 are the mean and variance of the sample count, respectively. Although many studies use numerical densities for this computation, Bez (2000) points out that the use of this index is sensible only when using counts. Meaning is lost when densities are used for calculating m and σ^2 due to the heterogeneity of units. More important, different patchiness values arise when using different density units. An example would be expressing numbers of individuals per m² vs. per 10 m² (Table 2, case A vs. B). Bez (2000) suggests the use of another index of aggregation (I_a) that is appropriate for densities. I_a is given by the following:

$$I_a = \frac{\sum_i z_i^2}{\left[s \left(\sum_i z_i \right)^2 \right]} \qquad (3)$$

where z_i is the density of organisms in a given sample and s is the size of the sampling unit used in the survey (note also that I_a is normalized and thus independent of total abundance in the sample area). The index assumes that the whole range of the species in question has been sampled; thus, the addition of zeros has no effect on the patchiness value (Table 2, case B vs. D). We use an index similar to Bez's I_a, modified for our sampling site and

scheme, because we cannot assume that we have sampled the whole range for any of the species here considered (Brinton et al. 1999). Our modified index is given by the following equation:

$$I_{mod} = \left[\frac{\sum_i z_i^2}{\left[s \left(\sum_i z_i \right)^2 \right]} \right] N \quad or \quad I_{mod} = I_a \cdot N \qquad (4)$$

where N is the number of stations sampled. For simplicity, we set s to 1 to generate a relative index, as approximately 1 m² was sampled by each net. Because sampling was done following similar protocols, the area sampled was similar for all our comparisons. For a different value of s, the index would simply be scaled in proportion to 1/s. Any bias arising as a consequence of our choice of s (Bez 2000) would be consistent across all size classes and species. Analogous to I_a, I_{mod} is robust to changing density units (Table 2, case A vs. B). It does not assume zero densities in unsampled areas, and it accurately expresses the same value of patchiness when two underlying distributions are the same yet one is more completely sampled (Table 2, case B vs. C). The index is sensitive to zeros (Table 2, case B vs. D) such that greater sampling resulting in zero density estimates count toward greater patchiness, unlike I_a, which assumes equal patchiness in both cases. I_{mod} is a more appropriate measure of patchiness for our study.

As mentioned earlier, not all species have the same distribution within the grid, and some species are known to experience changes in their north–south ranges as a function of oceanographic conditions (Brodeur 1986). Range reductions and expansions could affect the number of stations with zero individuals and thus artificially inflate the patchiness value. To account for this effect, we reduced the number of stations considered to the area within a cruise where each species occurred. We restricted our northern limit to the northernmost line with one individual at any station and the southern limit in the same way. The offshore limit was set by the westernmost station with one individual present. These considerations were applied to the range of every species for a given quarter (winter, spring, summer, and fall), which were the sampling blocks used in the computation of the patchiness index.

Table 2. Comparison of three patchiness indices: Lloyd's index of patchiness (P, Lloyd 1967), Bez's index (I_a, Bez 2000), and our modified version of Bez's index (I_{mod}). Cases A through D refer to different assumptions about the distributions of organisms (*see* Methods).

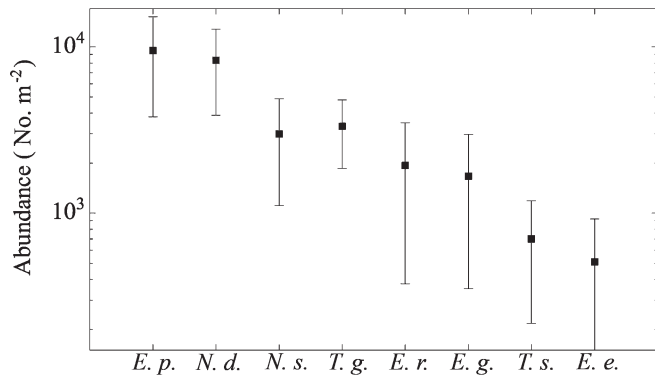| Case	Density of organisms	P (Lloyd's)	I_a	I_{mod}
A	8, 2	1.52	0.68	1.36
B	80, 20	1.7	0.68	1.36
C	80, 20, 80, 20	1.7	0.34	1.36
D	80, 20, 0, 0	3.84	0.68	2.72

Fig. 2. Average abundances for the eight numerically dominant species in the California Current System. Mean ± 95% C.I. for all cruises included in this analysis (note log scale). *E. p.* = *Euphausia. pacifica*; *N. d.* = *Nematoscelis difficilis*; *N. s.* = *Nyctiphanes simplex*; *T. g.* = *Thysanoessa gregaria*; *E. r.* = *Euphausia recurva*; *E. g.* = *Euphausia gibboides*; *T. s.* = *Thysanoessa spinifera*; *E. e.* = *Euphausia eximia*.

Patchiness values were calculated for the entire inhabited region and separately for the inshore and offshore domains (defined as in Fig. 1; Aksnes and Ohman 2009). We computed mean values as well as the coefficient of variation (C.V. $= \sigma_h^2/m_h$), where C.V. is the coefficient of variation and the subscript h refers to a hydrological variable) for chlorophyll *a* (Chl *a*) and temperature values from 30-m depth of all stations in the grid, together with Secchi disk depths, for all cruises from 1984 to present. For the physical–chemical data, we used C.V. instead of I_{mod} to express heterogeneity because hydrographic variables have continuous underlying distributions, and thus I_{mod} is not appropriate. The physical–chemical data originate from the CalCOFI database.

Statistical analysis—Analysis was carried out using Matlab 7.5. Mean patchiness values were computed by averaging the 40 patchiness estimates (from the 11 yr considered) for each species, along with respective parametric 95% confidence intervals (C.I.s). The Jonckheere–Terpstra test for ordinal data (Hollander and Wolfe 1973) was used to test the significance of the descending and ascending limbs of the patchiness–length curves. This statistic tests the null hypothesis of no sequence to the population medians against the alternative hypothesis that the population medians are ordered in a particular direction. For multiyear comparisons, as well as for the comparison before and after 1978, we used Kruskal–Wallis one-way analysis of variance.

Results

Patchiness vs. body size—The eight numerically dominant euphausiid species in this region have substantially different average abundances (Fig. 2; note log scale). Abundances are listed primarily in decreasing order in Fig. 2 and throughout the presentation of our results. A clear pattern of higher patchiness in the smallest size classes, followed by an abrupt decrease in patchiness and a

subsequent increase in the largest size classes, was evident for the four most abundant species: *Euphausia pacifica*, *Nematoscelis difficilis*, *Nyctiphanes simplex*, and *Thysanoessa gregaria* (Fig. 3). A similar but less pronounced pattern was suggested for the next four species (*Euphausia recurva*, *Euphausia gibboides*, *Thysanoessa spinifera*, and *Euphausia eximia*; Fig. 3).

In order to test the null hypothesis of size-independent patchiness, we evaluated the initial decrease and the subsequent increase in patchiness separately. For the descending limb of the curve, we considered the first four size classes (Fig. 4a). A significant decrease in the patchiness index I_{mod}, as measured by the Jonckheere–Terpstra test for ordered alternatives, was detected for six of eight species ($p < 0.05$; Fig. 4a). The initial decline was not significant ($p > 0.05$) for either *E. gibboides* or *T. spinifera*. For the ascending limb of the curve, we considered the length class at which maximum patchiness was attained, along with the preceding four size classes (Fig. 4b). For six of eight species, we observed increasing patchiness with increasing body size of adults ($p < 0.01$; Fig. 4b). The observed increase was not significant ($p > 0.05$) for either *T. spinifera* or *E. eximia*.

Arrows on the abscissa on Fig. 3 indicate the body length at the first appearance of secondary sexual characteristics for each species from Brinton et al. (1999). The increase in patchiness of larger body–sized individuals did not coincide with this size class; however, there was usually an inflection point denoting an increase in mean patchiness 3–5 mm after the first onset of secondary sexual characteristics.

Temporal differences in patchiness—We investigated temporal variability in patchiness at three different scales. We first examined seasonal differences in aggregation for all species and found no consistent seasonal differences in patchiness as a function of body size for any of these species (not shown).

We also investigated patchiness differences among the years of our study (Fig. 5) specifically with reference to the strong El Niño–Southern Oscillation (ENSO) conditions of 1958–1959. Neither 1958 nor 1959 stands out for either abnormally high or low patchiness. However, 1955 showed generally higher patchiness in at least some size classes for all species. The year 1955 was characterized by early and intense upwelling (Brinton 1976). These differences, however, were not statistically significant for any of the euphausiid species ($p > 0.05$).

Finally, we examined aggregation patterns before and after the cool-to-warm transition in the northeastern Pacific from 1976 to 1977. For this purpose, we compared patchiness for the years prior to the transition (1953–1959 plus 1969) vs. those afterward (1978, 1984, and 1991). Results were significant for only some size classes of some species (range 0–4 size classes, $p < 0.05$), although no consistent relationship was found in these differences among species (not shown).

Spatial differences in patchiness—We divided the study region into two subregions, designated inshore and offshore (Fig. 1), in order to assess whether euphausiid
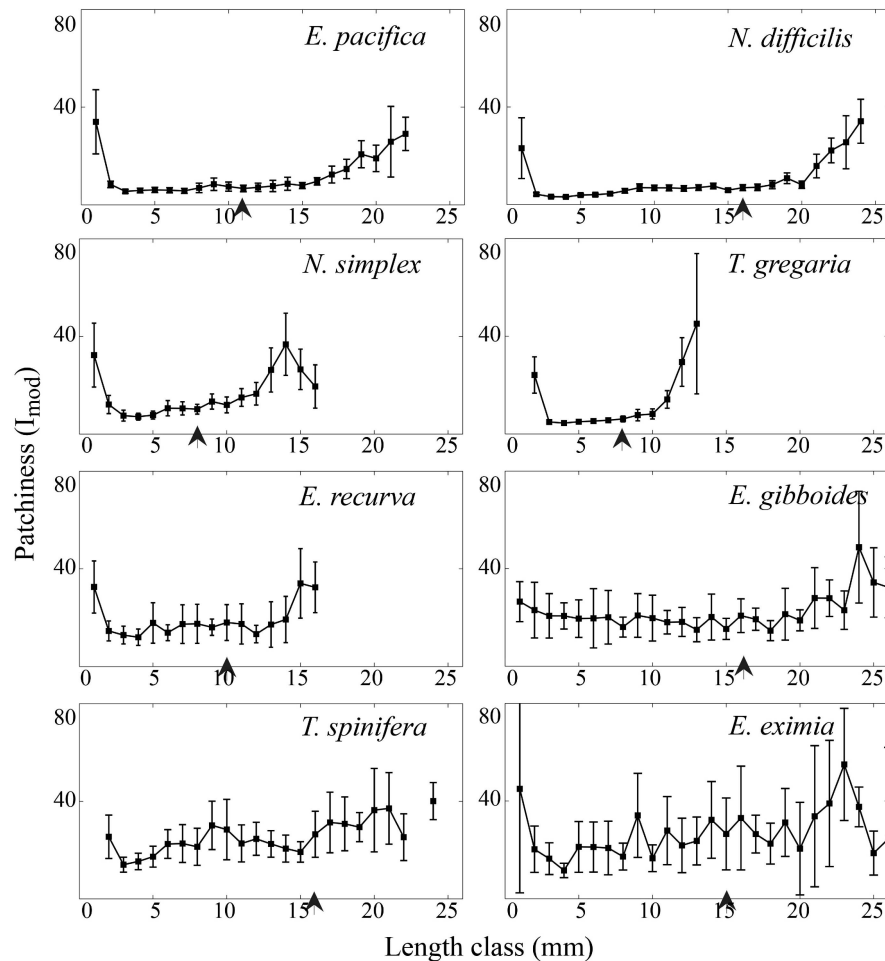
Fig. 3. Patchiness (I_{mod}) as a function of euphausiid length (mean $\pm$ 95% C.I.). Arrows indicate length at onset of sexual maturity.

patchiness varied with spatial differences in heterogeneity of the physical–chemical environment. The inshore region was, on average, cooler with higher Chl *a* concentrations and shallower Secchi disk depths than the offshore (Fig. 6a–c) as would be expected since much of this region is influenced by coastal upwelling in the vicinity of Point Conception. The C.V. of Secchi disk depth and temperature was elevated inshore relative to offshore stations ($p < 0.05$, Wilcoxon signed rank test; Fig. 6d–f), but there was no significant difference in C.V. of Chl *a* ($p > 0.05$). Calculation of euphausiid patchiness in the corresponding two spatial regions revealed that when the ascending limb and descending limbs of the curve were present, they were found in both inshore and offshore regions for each species (Fig. 7). When there was a significant difference ($p < 0.05$) between the two patchiness curves, the inshore portion of a species population was always characterized by higher patchiness with respect to the offshore counterpart. The two smallest transition-zone species, *T. gregaria* (cool) and *E. recurva* (warm), showed increasing departures between inshore and offshore patchiness curves with increasing size (Fig. 7).

Reproductive differences: Free spawners vs. brooders—We investigated the hypothesis that patchiness–length

curves differ between species displaying different reproductive modes. For this purpose, we considered the two egg-brooding species (*Nematoscelis difficilis* and *Nyctiphanes simplex*) in relation to the remaining six species, all of which spawn their eggs freely into the water column. There was no consistent difference in patchiness pattern between the two reproductive modes (*see* Fig. 3). In Fig. 8, we more closely compare two free-spawning species (*E. pacifica* and *T. gregaria*) with two egg-brooding species (*N. difficilis* and *N. simplex*). These pairs of species are the most comparable in abundance and also in having one member that reaches a relatively large adult length (22 mm and 26 mm for *E. pacifica* and *N. difficilis*, respectively) and one of each that reaches a relatively small adult length (13 mm and 16 mm for *T. gregaria* and *N. simplex*). All four species have well defined U-shaped patchiness–length curves (Fig. 8; $p < 0.01$; from Fig. 4), and the overall magnitude of patchiness was similar.

Discussion

We reject the hypothesis of size-independent patchiness for seven of eight species of numerically dominant California Current euphausiids. Only *T. spinifera* showed
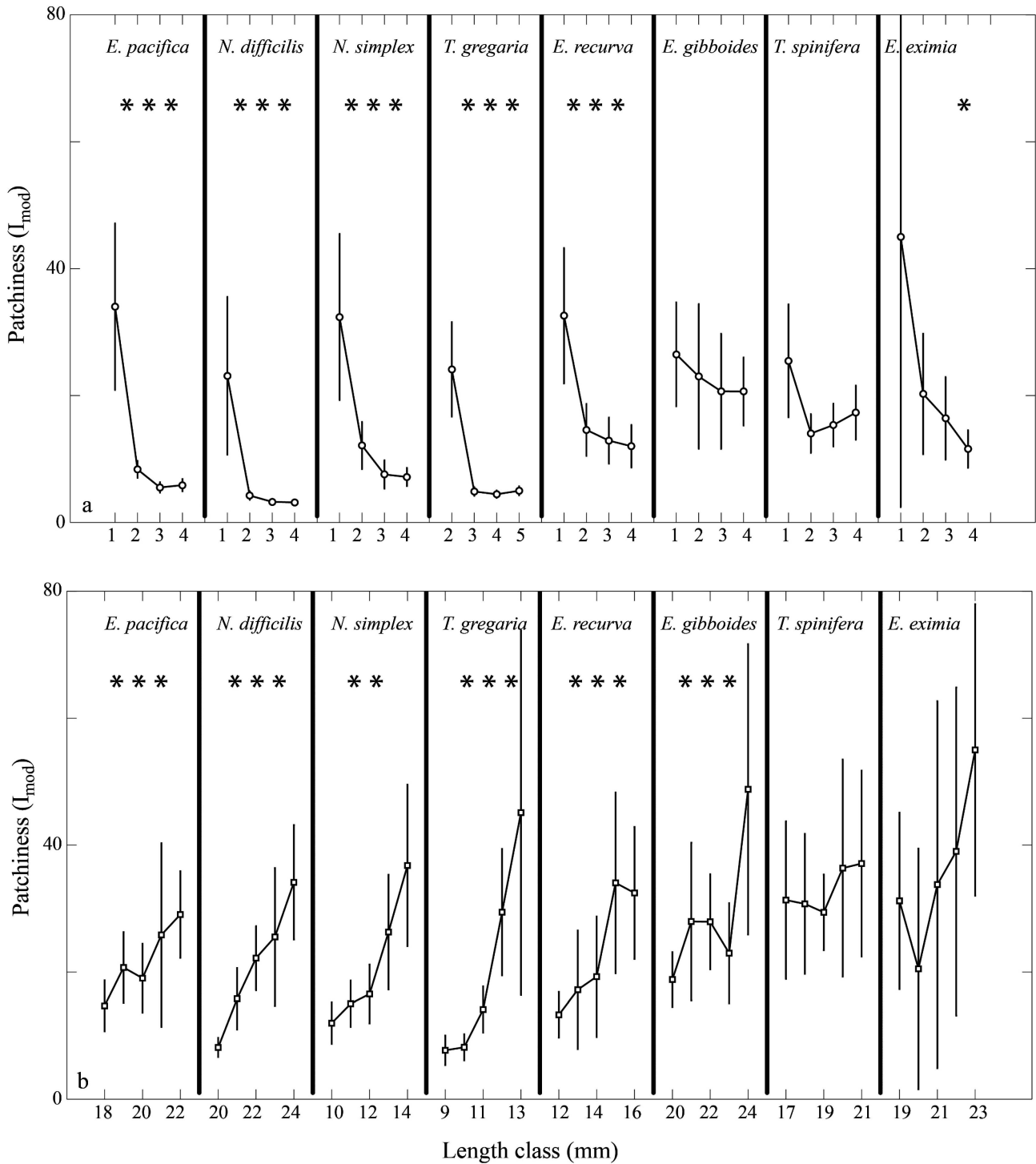
Fig. 4. (a) Initial descending limb and (b) final ascending limb of euphausiid patchiness vs. total length. Statistical significance of Jonckheere–Terpstra test: *** $p < 0.001$; ** $p < 0.01$; * $p \leq 0.05$.

neither an initial decrease in patchiness for the smallest size classes nor a subsequent increase in patchiness for the largest size classes or both. The most common pattern we detected was a U-shaped trend with body size, character-ized by elevated patchiness in the smallest size classes, a decline to minimum values in intermediate size classes, and

an increase for the largest size classes after the onset of reproductive maturity.

The mechanisms that lead to zooplankton patchiness can be broadly classified into those of physical (e.g., turbulence, shear, habitat heterogeneity) and those of biological (e.g., intraspecific and interspecific interactions) origins. Our
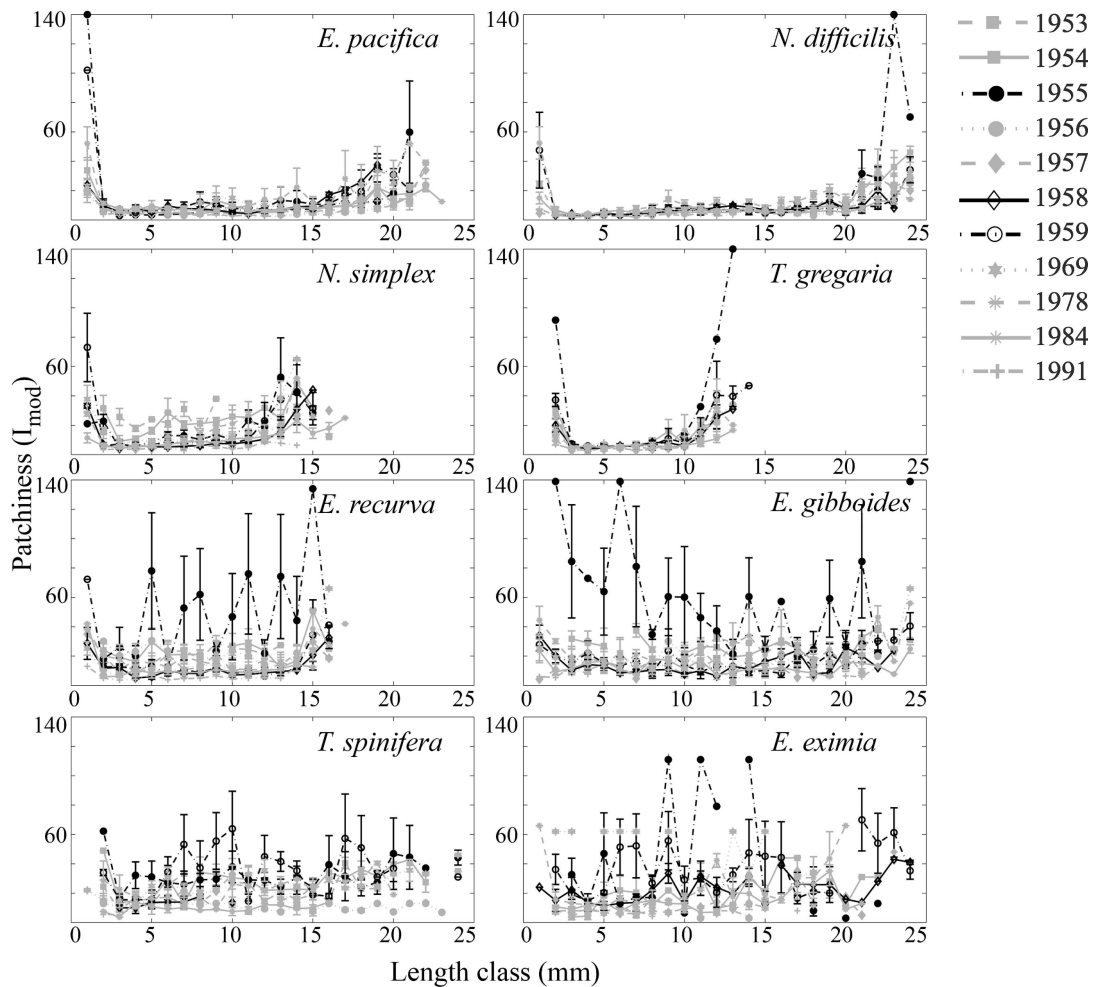
Fig. 5. Interannual variations in patchiness vs. euphausiid total length.

interpretation of the mechanisms leading to the U-shaped pattern observed in the euphausiid patchiness–length curves in some respects parallels patterns described previously in changes of fish patchiness with ontogeny (Hewitt 1981). The descending limb of the patchiness curve is most consistent with the consequences of physical processes: turbulent diffusion would lead to dispersion of organisms and a substantial decrease in larval patchiness with body size. The smallest size classes considered here correspond to the calyptopis life history phase (eggs, nauplii, and metanauplii were not collected quantitatively by the net mesh used). Development time to reach the calyptopis stage is highly variable among species (especially with different reproductive strategies) and is temperature dependent but seems to be on the order of hours to 10 d (Gomez-Gutierrez 2002, 2003). Calyptopes are able to both feed and swim; however, their ability to determine their position in the water column actively or to respond to conspecifics is greatly reduced given their small size and undeveloped pleopods (Brinton et al. 1999). We infer that the very high initial patchiness of the smallest size classes is a result of the aggregation of spawning adults, with passive dispersion of weakly swimming larvae assumed to be the

dominant process leading to subsequent low I_{mod} values as the organisms develop and grow.

In contrast, the ascending limb of the patchiness curve is inconsistent with physical processes alone. If the only mechanisms affecting aggregation were physical processes, such as advection and diffusion, we would expect the patchiness curve to approach a generally low, uniform pattern at large body size as the distribution of the larger and older animals becomes more evenly spread out over time. Instead, we see increasing patchiness in the larger size classes of all euphausiids. Furthermore, the onset of this pattern is related to interspecific differences in adult body size rather than a fixed absolute size for all species. The ascending limb of the patchiness–length curve is likely governed by biological processes. We can subdivide the likely biological processes into those where euphausiids respond to one another (e.g., reproductive aggregations, schooling for hydrodynamically efficient swimming) and those in which euphausiids respond to external stimuli (e.g., changes in the physical–chemical environment, prey resources, or the predator field).

Active aggregation into cohesive units has been extensively reported and studied for the Antarctic species
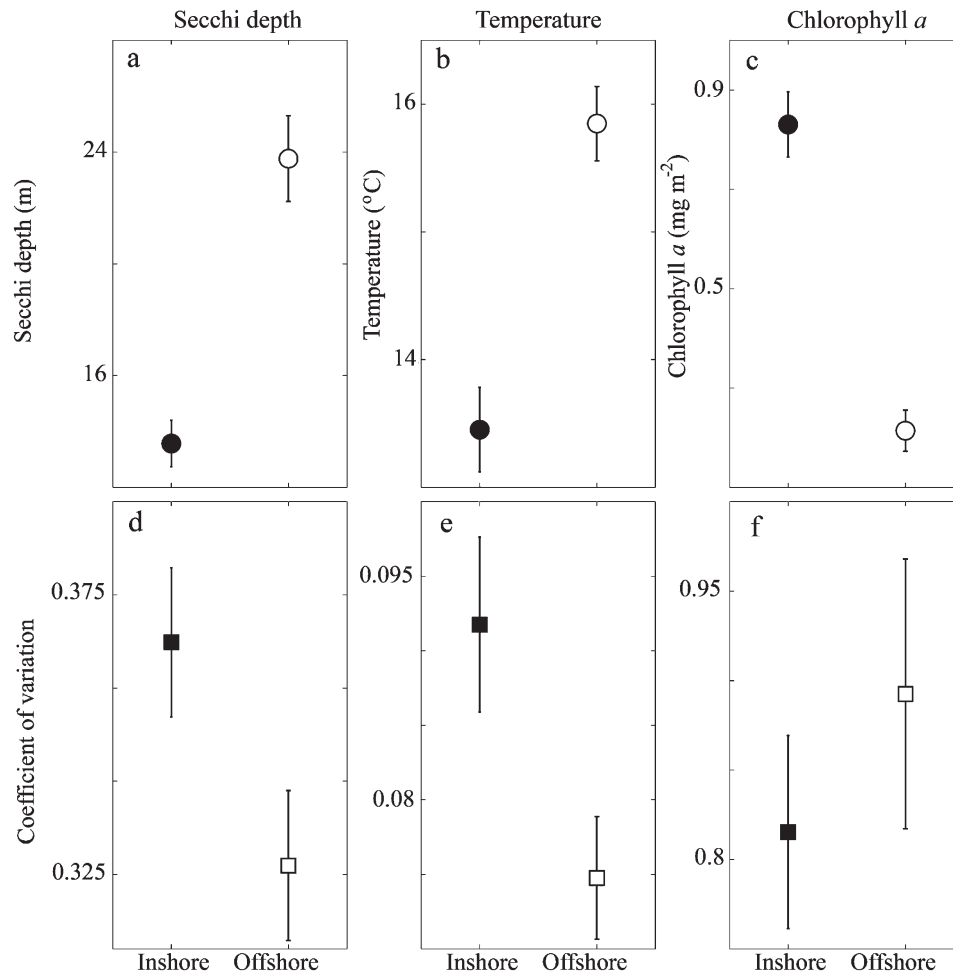
Fig. 6.   Upper panels: contrast between the inshore (black) and offshore (gray) regions in (a) Secchi disk depth, (b) temperature, and (c) chlorophyll a (Chl a), the latter two measured at 30-m depth (mean ± 95 C.I.). Lower panels: contrast between the coefficient of variation (C.V.) in the inshore vs. offshore region (mean C.V. ± 95 C.I.) of (d) Secchi disk depth, (e) temperature, and (f) Chl a.

Euphausia superba (Hamner et al. 1989; Watkins and Murray 1998). The distribution pattern of each life history stage of this species has also been argued to be a product of both physical and biological processes (Nicol 2006). Differential aggregation with size has also been reported for this species (Watkins et al. 1992; Johnson and Tarling 2008). These aggregations are hypothesized to confer antipredatory benefits and increase foraging efficiency (Hamner and Hamner 2000), optimize food capture and energy expenditure (Ritz 2000), and also to confer reproductive benefits as reported for many species of euphausiids (discussed below). The California Current species have not been reported to form true schools (i.e., individuals with parallel orientation and constant nearest-neighbor spacing) in situ, and therefore we do not consider it likely that schooling benefits such as hydrodynamic efficiency are the ultimate factors leading to their aggregation. A few California species, however, are known to form visible aggregations that do not have the organized character of a school, a form of aggregation we call a "swarm."

Although the absolute scale of patchiness cannot be inferred from the index of patchiness we have used, the station spacing at which we have sampled must be kept in mind while interpreting our results. The shortest spacing between two CalCOFI stations occurs inshore and is on the order of 20 km (Fig. 1). In general, our sampling is on the order of 20–60 km (considering the spacing of stations both inshore and offshore). For the species for which swarming has been documented, daytime surface swarms occur occasionally (Brinton and Townsend 2003), and nighttime dense aggregations have also been reported (H. C. Shin pers. comm.). These types of swarms would contribute to our measure of patchiness. Therefore, although the aggregations our metric has detected are, in principle, at the mesoscale, our index would also be influenced by smaller-scale processes.

Surface swarms of euphausiids for sexual purposes have been observed in different regions of the northeastern Pacific for a number of species analyzed here (Endo et al. 1985; Smith and Adams 1988; Gendron 1992). In our case, we noted that the onset of increased adult patchiness began not at the size of first sexual maturity but, rather, a few size classes later. A better metric of the reproductive status of the population than initial onset would be the length at which 50% of individuals have attained reproductive
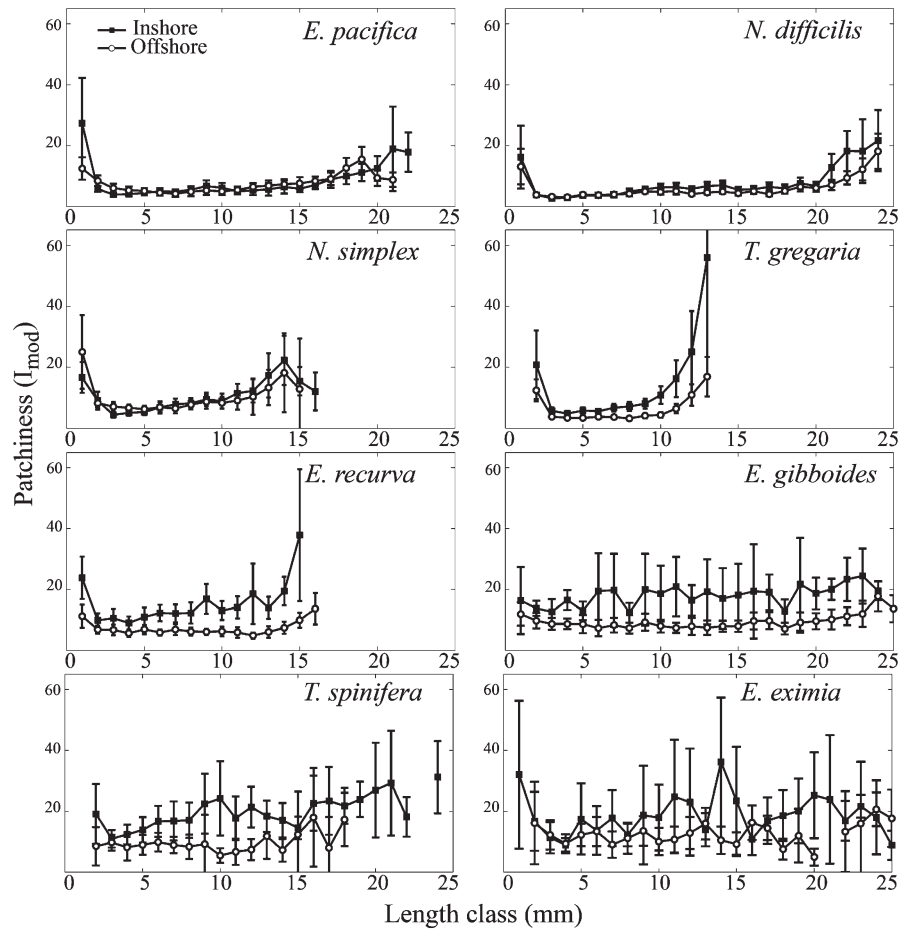
Fig. 7. Contrast between the inshore (black) and offshore (gray) regions in patchiness (I_{mod}) vs. total length for the eight euphausiid species (mean ± 95 C.I.).
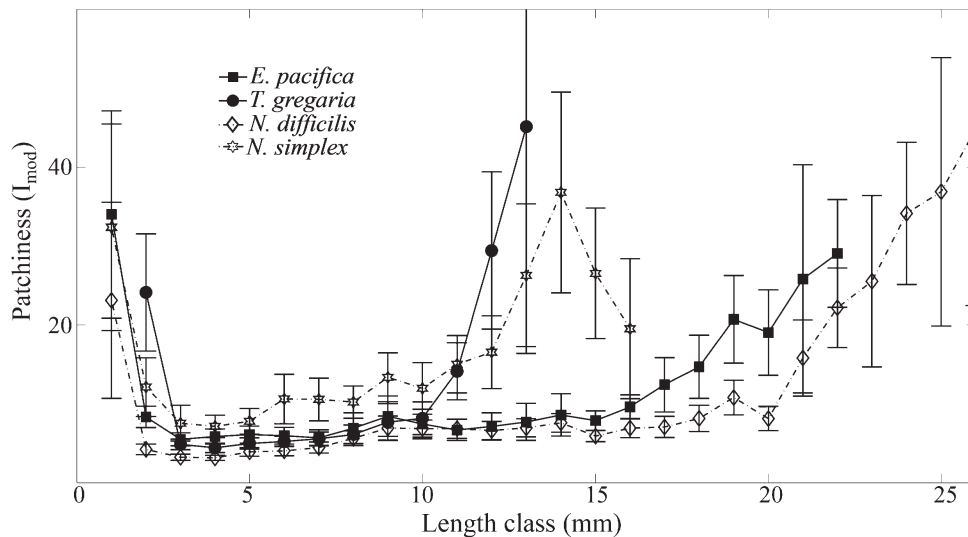

Fig. 8. Patchiness (I_{mod}, mean ± 95 C.I.) vs. total length for euphausiid species displaying two reproductive modes: broadcast spawners (black; *E. pacifica* and *T. gregaria*) and egg brooders (gray; *N. difficilis* and *N. simplex*).

maturity, though we do not have pertinent data available. The consistent increase in patchiness at a size 3–5 mm beyond the initial onset of maturity suggests that reproductive benefits cannot be ruled out as an explanatory factor.

Diel vertical migration (DVM) behavior of adult euphausiids could potentially also affect the observed pattern. Segregation between larval and adult stages has been shown to occur because of the migration of adults in areas of intense upwelling characterized by sheared flows, via transport of larvae offshore and retention of adults onshore (Mackas et al. 1997). Depth and timing of DVM have also been shown to vary with adult size, with larger organisms descending deeper in the water column (Bollens et al. 1992) and spending proportionally less time at the surface at nighttime (De Robertis 2002). However, two nonmigrating species, *N. difficilis* and *T. gregaria*, have very strong ascending limbs in their patchiness curves (Fig. 3). DVM therefore seems unlikely to be the principal mechanism underlying the pattern we observed.

Where patchiness is exclusively a vectorial response (Hutchinson 1953), that is, a response to common external stimuli in the environment, a general expectation is that aggregations of organisms would be enhanced where the external stimuli are heterogeneous. We observed that the inshore region we analyzed was more heterogeneous than the offshore region (Fig. 6) with respect to temperature and water column transparency (which influences encounter distances with visually hunting predators). For some euphausiid taxa, we detected elevated patchiness in the inshore region, suggesting that increased environmental heterogeneity does indeed contribute to the nonrandom distribution of the organisms. However, it is noteworthy that the ascending limb of the size-dependent patchiness curve also occurred in the offshore region, where the external environment showed less heterogeneity. Hence, we conclude that there is a biological cause of patchiness in larger-sized euphausiids that persists independent of the external environment but can be enhanced by it. This is consistent with modeling studies that have shown individuals in homogeneous environments displaying behavior that leads to patchy distributions (Deutschman et al. 1993). Random movement coupled with predator–prey interactions has also been shown to produce aggregated distributions in homogeneous environments (Deutschman et al. 1993).

Euphausiid aggregations in the California Current have been associated with topographic breaks (Schoenherr 1991; Croll et al. 2005), along continental shelf breaks (Simard and Mackas 1989; Mackas et al. 1997) and submarine canyons (Croll et al. 2005), and around the vicinity of the Channel Islands (Croll et al. 1998). In the present study, the region we have defined as "inshore" comprises the Southern California Bight, which overlies a region of complex bathymetry with deep basins, seamounts, ridges, and submarine troughs (*see* Fig. 1). Such topographic features could influence euphausiid patchiness through alterations in flow, nutrient enrichment, or seamount-associated predators (Genin et al. 1988, 1994). This inshore region also is a region of high abundance of planktivorous

fishes and elevated mortality of the copepod *Calanus pacificus* (Ohman and Hsieh 2008).

If euphausiid predators are size selective, they can cause differential mortality that could lead to the patterns discussed here. Baleen whales foraging on euphausiid aggregations in Monterey Bay, California, have been shown to be strongly size selective (Croll et al. 2005). A comparison between size frequency distributions of euphausiids in the water column and euphausiid remains in fecal matter from whales feeding in the same area revealed that blue whales preferentially selected larger body–sized euphausiids. Consumption by these and other baleen whales accounts for a significant fraction of plankton production in the California Current (Barlow et al. 2008). Many other organisms in the California Current that feed on euphausiids (including fishes, seabirds, squid, and others) may also show size-dependent rates of encounter and consumption of euphausiids. Size-dependent predation could lead to size-dependent patchiness through at least two specific mechanisms. Consumption by predators would lead to "gaps" in distributions as a direct consequence of prey removal, and this pattern would increase with body size because of cumulative mortality. Alternatively, the enhanced predation risk to larger body–sized euphausiids (De Robertis 2002) would select for more highly developed aggregation responses in successively larger size classes.

Concerning interannual differences in patchiness, 1955 was a year of abnormally high upwelling with noticeable effect on the population biology of *E. pacifica* (Brinton 1976). In light of the pattern of somewhat higher patchiness inshore, as well as observations of associations between euphausiid aggregations and regions of high chlorophyll (Croll et al. 2005; Ressler et al. 2005), perhaps years with higher production are associated with greater spatial variability of production and/or predators and higher euphausiid patchiness (Brodeur and Pearcy 1992). The ENSO included in our analysis (1958–1959) did not strongly affect euphausiid spatial patchiness, but we cannot conclude that ENSO consistently has no effect on euphausiid patchiness from this one event alone. In addition, ENSO conditions can surely affect euphausiid species ranges, modifying their north–south limits in the California Current (Brodeur 1986).

The lack of a clear difference in the U-shaped pattern with spawning mode (egg brooding vs. broadcast spawning) may constitute a true departure of euphausiids from fishes. For euphausiids, patchiness of the smallest size classes was similar between free spawners and brooders, and neither the magnitude of decrease in the subsequent size classes nor adult patchiness had any relationship to spawning mode. In contrast, differences in fish patchiness–age curves have been hypothesized to be linked to differences in the habitat into which eggs are spawned, specifically demersal vs. pelagic spawning (McGurk 1987), or to the inherent differences arising from these two spawning modes. For pelagic fishes, the patchy distribution of eggs and young larvae is introduced by the highly aggregated reproductive behavior of the adults, where fertilization and spawning occurs almost simultaneously. Alternatively, demersal eggs are laid on a substrate and

must incubate over some period of time (Matsuura and Hewitt 1995); their distribution would not necessarily follow adult aggregation as closely as for pelagic fishes. In a similar way, brooding euphausiids carry egg sacs with developing embryos, and larval hatching occurs hours to days after reproductive aggregations take place. However, the smallest size class we consider corresponds to calyptopis I, which is two or three stages removed from the egg stage (for brooders and free spawners, respectively). A difference in patchiness arising from spawning mode would probably be most pronounced in the earlier naupliar and metanaupliar stages. Turbulent diffusion may have eliminated any difference in patchiness, if present, by the time organisms have developed into the smallest size classes considered here. Complete sampling of the youngest developmental stages would be needed to address this question.

In conclusion, we have established a U-shaped pattern of patchiness as a function of body length in California Current euphausiids. The descending limb of the euphausiid curve is consistent with turbulent diffusion acting to diminish the local patches of eggs and the youngest larval stages generated by spawning adults. The ascending limb of the patchiness curve is consistent with predator-induced aggregation via mechanisms such as differential mortality and predator avoidance behavior. Spatial differences in habitat heterogeneity may secondarily modify the patchiness of euphausiids.

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