Journal of Experimental Marine Biology and Ecology 407 (2011) 226–233

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Seafloor mapping and landscape ecology analyses used to monitor variations in spawning site preference and benthic egg mop abundance for the California market squid (*Doryteuthis opalescens*)

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ARTICLE INFO

Article history:
Received 11 November 2010
Received in revised form 15 June 2011
Accepted 17 June 2011
Available online 23 July 2011

Keywords:
Ecosystem based management
Marine protected areas
No-take zones
Reproduction
Sidescan sonar
Squid fishery

ABSTRACT

The California squid fishery is concentrated largely on nearshore squid spawning aggregations. Because of this practice a central concern for sustainable squid fisheries in California is to determine whether reproductive activities and subsequent egg laying occur at rates that are sufficient to support harvestable populations of this sub-annual species. Using high-resolution data collected via acoustic mapping methodology, we estimated a 99% decrease in egg mops abundance from 2005 to 2007. Sidescan sonar images from detailed benthic mapping suggest that although squids prefer a sandy substrate as their primary egg mop habitat, the depths across which egg mops were distributed differed significantly between surveys and spatial distribution of egg mops varied across years on this large spawning ground. Our results suggest that sidescan sonar surveys could serve as an important tool used to aid sustainable management of the California market squid fishery through the monitoring, designation and adaptive management of seasonally variable no-take spawning zones and can help in developing stock assessments of this commercially important species.

1. Introduction

The life history characteristics of some marine species make them more susceptible to overexploitation than others. For example, species that form spawning aggregations, such as many species of squid and grouper, are extremely vulnerable to overexploitation due to fishing practices that target their annual spawning grounds (Coleman et al., 1996). In order to develop successful management strategies for species that aggregate during spawning, there is a need for more and better data on variation in the species' spatial and temporal use of spawning habitats. The California market squid, (*Doryteuthis* (formerly *Loligo*) *opalescens*), a group spawner, potentially offers an ideal sustainable fishery due to their semelparous (spawn once and die) life history. As long as *D. opalescens* are allowed to spawn prior to being caught, the sub-annual recruitment can sustain the population (Hanlon et al., 2004; Hibberd and Pecl, 2007).

Like many loliginid squid fisheries worldwide, *D. opalescens* are captured directly on spawning sites (Butler et al., 1999) where they are lured closer to the surface using high wattage light boats and caught with large purse seines (Maxwell et al., 2004; Zeidberg et al., 2006) that can contact the seafloor when deployed over shallow spawning grounds (R. Kvitek pers com). The consequences of fishing on spawning grounds are not completely known but of serious concern (Hanlon, 1998; Sauer, 1995) because they can potentially include disruption of *D. opalescens'* complex mating and egg laying behaviors (Hanlon et al., 2004; Hanlon and Messenger, 1996) as well as dislodging egg mops from their attachment to the sandy substrate.

Doryteuthis opalescens is a comparatively small squid that inhabits the middle trophic level in the California and Alaska current systems along the coast of North America (Morejohn et al., 1978; Zeidberg et al., 2006). They are found from the southern tip of Baja California to southeastern Alaska (Hixon, 1983). Market squid is an important species for both the commercial fishery and a vital forage species for a large number of birds, mammals, and fishes (Zeidberg et al., 2006). They spend the majority of their 6–9 month lifespan offshore, returning inshore solely to spawn (Hixon, 1983; Yang et al., 1986). During spawning, females lay a cluster of egg capsules in nearshore, shallow waters on sandy substrates (Hixon, 1983).

As a possible solution to potentially harmful effects of fishing directly on spawning sites, the California Department of Fish and Game (CDFG) recommended the adoption of no-take spawning areas (Mangel et al., 2002). The Marine Life Protection Act (MLPA) in California has helped to protect some important spawning areas through the designation of marine protected areas; however, sites where *D. opalescens* consistently spawn (records date back more than 100 years; Fields, 1965), are not protected from fishing pressure. As a

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doi:10.1016/j.jembe.2011.06.017

monitored species there are no mandatory harvest limits but there are seasonal catch limitations, monitoring programs, and a permit system (NMFS, 2009). Overall, the lack of data on squid population size, fishing effort, and the spawner-recruit relationship has made management unorthodox and difficult (Maxwell et al., 2005). The methods used in this study could provide a means for managers to estimate biomass of both reproductive output and the population and, as a result, come up with stock assessments for this commercially important species.

Previous studies have demonstrated that sidescan sonar can be used to accurately map the locations of spawning grounds for *D. opalescens* (Foote et al., 2006). The purpose of this study is to build upon those results from previous studies and begin to look at how the use of sidescan sonar to map the location of egg mops can answer questions about the ecology of *D. opalescens* by testing the following hypotheses:

Hypothesis 1. *D. opalescens* show a consistent interannual preference for specific habitat types and depths.

Hypothesis 2. *D. opalescens* consistently spawn in the same location each year, and do not use immediately adjacent areas of similar depth and substrate type.

Hypothesis 3. Backscatter data collected by a hull mounted multi-beam system can be used as an accurate and efficient way to map *D. opalescens* spawning grounds.

Understanding spatial and temporal habitat use by spawning *D. opalescens* is critical in determining whether static or dynamic no-take spawning zones would be the most effective strategy for sustainable management of this valuable fishery.

2. Materials and methods

2.1. Data acquisition and processing

Five consecutive sidescan sonar and video surveys of squid egg beds were conducted over three years on the traditional fishing grounds of Monterey, CA in the southern portion of Monterey Bay. The survey dates were: summer 2005 (31 May 2005–1 June 2005); spring, summer, and fall 2006 (28 April 2006–2 May 2006, 9 June 2006–15 June 2006, 1 September 2006–2 September 2006); and summer 2007 (27 May 2007–2 June 2007). The summer surveys from each year were used for detection of inter-annual variation in egg mop distribution and the three surveys completed in 2006 were used to estimate intra-annual variation. All data were collected within a 1.46 km^2 study area along the southeast shore of Monterey Peninsula (36°37′02″ N, 121°53′27″ W). The squid egg beds are predominantly found in the sandy substrates beyond the nearshore kelp beds. Once mapped, we verified the locations of the squid egg beds using a Deep Blue Pro color camera with a 3.6 mm wide-angle lens, focus fixed at 2.54 cm and a National Television System Committee (NTSC) composite video image resolution of 480 TV lines. Survey methods for mapping the egg beds are described in detail in Foote et al. (2006).

In addition to sidescan sonar, multibeam sonar data were collected within the study area using a pole-mounted Reson SeaBat 8101 multibeam sonar system. Unlike sidescan sonar, which collects information on the intensity of return of the acoustic signal and can distinguish between different substrate types on the seafloor (i.e. rock will return a stronger acoustic signal than sand), multibeam sonar simply records the two-way travel time of the sound to calculate the depth of the seafloor at 1.5° intervals across a 150° swath yielding high-density depth sounding data across the entire survey area. Following acquisition, the multibeam data were imported into CARIS HIPS software where they were processed using standard hydrographic data cleaning procedures (see CARIS, 2006 for a description) and the data were exported from CARIS as regularly spaced (2 m) XYZ points. These XYZs were converted into a digital elevation model (DEM) in ESRI Grid format for GIS analysis.

Because *D. opalescens* show a preference for particular habitat characteristics when depositing their eggs on the seafloor (Hanlon, 1998; Hanlon et al., 2004; Hurley, 1977; Zeidberg and Hamner, 2002), the following habitat rasters were algorithmically derived from the DEM (ArcGIS 9.2 ESRI®) for determining the relationship between spawning location and habitat: slope, vector ruggedness measure (VRM), and topographic position index (TPI). A slope raster was derived from the bathymetric DEM using the ArcGIS Spatial Analyst extension. A VRM grid, which measures the complexity of the seafloor, was created using the Terrain Tools extension for ArcGIS 9.2. The final habitat metric derived was topographic position index (TPI), which indicates the position of a given point in the overall surrounding landscape (i.e. peaks, slopes, valleys, crevices, etc.). The TPI analysis employed in this study was done using the algorithm of Weiss (2001), which uses an annulus ("donut") shaped neighborhood.

2.2. Using sidescan to quantify squid eggs

The digital images from each sidescan survey were brought into (ArcGIS 9.2 ESRI®) to quantify the visible egg beds. Prior to the GIS analysis, a single technician was trained to distinguish between egg beds and other anomalies in the image such as rocks, sediment changes, and artifacts by comparison of georeferenced video and sidescan sonar imagery. Once trained, the technician traced polygons around each individual egg mop for all of the surveys without further aid of the video data. Area was calculated for each egg mop to give the total coverage of egg mops within each sidescan survey. Over 18,000 egg mops were identified during the three year study.

2.3. Squid egg depth distribution

To determine if *D. opalescens* has a depth preference within which it deposits eggs, the egg mop polygons from each survey were used to test for differences in the depth distribution between and within years. The Zonal Statistics tool within the Spatial Analyst Tools in ArcGIS 9.2 was used to find the average depth for each egg mop polygon from all the surveys. These depth values were then exported from ArcMap for statistical analysis.

To determine whether the data met the assumptions for an ANOVA, the distribution of the depth data were compared to the normal distribution using the Kolmogorov–Smirnov test. Because the data were significantly different from the normal distribution ($p<0.000$), a non-parametric Kruskal–Wallis test was used to determine if there was a significant relationship between distribution and egg mop depth.

2.4. Spatial distribution of egg mops

To determine if there was significant spatial clustering of egg mops within each of the years used in this study, separate Ripley's K analyses were used. Ripley's K provides not only an estimate of spatial clustering within an ecosystem but can provide insight on the scales across which clustering occurs and the potential environmental processes that drive spatial patterning in ecological systems by using the distance between all pairs of points in the study area (Kuuluvainen et al., 1996; Ripley, 1981). Ripley's K analyses were completed using the Multi-Distance Spatial Cluster Analysis (Ripley's K Function) within ArcGIS 9.2. If significant clustering was found, a Chi-square test of association was then conducted for the following habitat variables at each spatial scale to ascertain if clustering was significantly associated with different categorical levels of depth, slope, vector ruggedness measure (VRM), and topographic position index (TPI). Chi-square residuals were then analyzed to estimate the relative contribution of each within variable category (e.g. depth category) to egg mop clustering at each spatial scale.

2.5. Multibeam backscatter as a tool for detecting egg mops

In May of 2010, we used a Reson 7125 sonar system to collect multibeam and backscatter data over the squid spawning study area to determine if a hull mounted sonar system could be used to map the distribution of *D. opalescens* egg beds. The Reson 7125 collects depth and backscatter data using 512 beams at 0.5° intervals across a 128° swath. The backscatter data are similar to towed sidescan data but are collected simultaneously with the multibeam depth data and, rather than having a single time series of intensity data for the port and starboard side, each of the 512 beams has a time series providing high-resolution, precisely georeferenced intensity data. To collect the multibeam backscatter data, we ran multiple parallel transects across the survey area and used the realtime display of the backscatter to record the location of potential egg beds. Then, using a drop camera, we went back to those areas of presumed presence and absence of egg mops and compared those results to what we were seeing in the backscatter.

3. Results

3.1. Variation and trends in egg mop abundance

Within the survey area (Fig. 1), there was a decrease in the total number of *D. opalescens* egg mops and the area of coverage identified in the sidescan mosaics from the first survey to the last. Over 18,000 *D. opalescens* individual egg mops were identified within the sidescan data collected during the three year study. Each survey covered the same 1.46 km^2 area. The first survey, June 2005, had the greatest number of egg mops (7,221) covering an area of 3075 m^2. The April/May 2006 survey found 5555 egg mops (2,231 m^2) but only 379 egg mops were identified in May 2007 covering 94 m^2 within the survey area. May 2007 experienced a 95% decrease in total number of egg mops and 97% decrease in the total area covered by the egg mops compared to the June 2005 survey results.

3.2. Squid egg depth distribution

The results from the Kruskal–Wallis test show that the egg mop depth distributions from one or more of the five surveys used in this

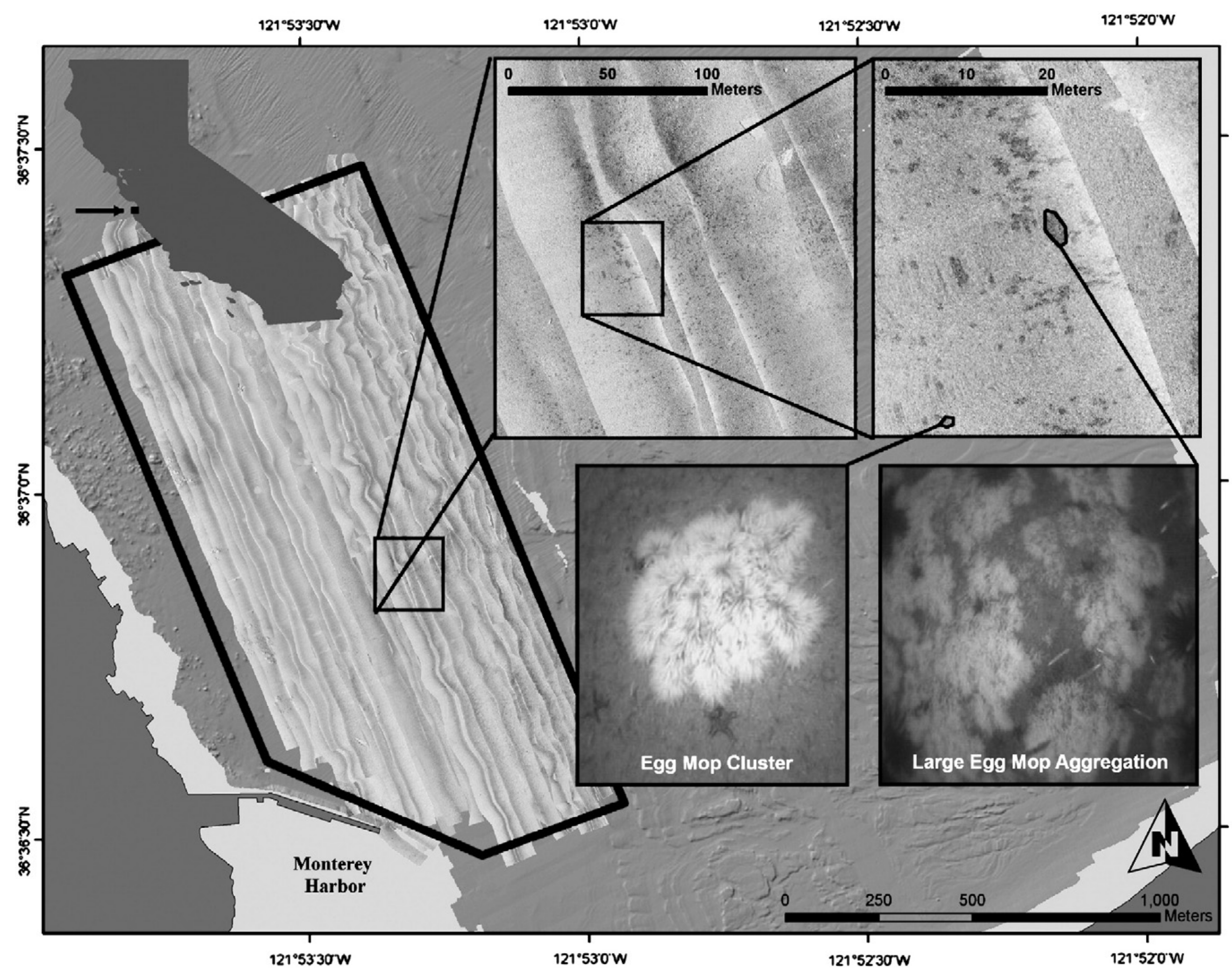

Fig. 1. A sidescan sonar mosaic from June 2006 with extent boxes showing egg mops identified from the mosaic. The dark splotches represent squid egg mops detected in the sidescan imagery. The images of the egg mops are "video frame grabs" from the video footage (recorded at 30 frames/s) used to ground-truth the site. The gap in data between the land and where the multibeam shaded relief begins is due to the surf zone and the inability to map in that area (Multibeam imagery in shaded relief: image illumination azimuth 315, elevation 45, resolution 2 m. Sidescan imagery in grayscale, resolution 0.1 m. Coordinate system: Geographic WGS 1984).

study were significantly different ($p<0.000$, $n=5$). To determine which surveys were significantly different from each other, a series of Mann-Whitney U tests was used to make pair-wise comparisons. Each egg mop distribution was found to be significantly different from each other ($p<0.000$, $n=5$) for every pair-wise comparison.

3.3. Spatial distribution of egg mops

Ripley's K analysis revealed significant clustering of egg mops across all sample years ($p<0.001$). In 2005, the egg mops were aggregated adjacent to the sand/rock interface in the shallowest portion of the study area with an average depth of 19 m. There was significant clustering across all spatial scales but the peak clustering occurred at a scale of approximately 60 m. The clustering of egg mops in 2006 was aggregated in the center of the study area surrounded by a scattering of egg mops. The observed clustering pattern was significant across all scales with the statistical significance of egg mops increasing as the sampling scale increased. In 2007, the clustering pattern was not as visually distinct but still statistically significant across all spatial scales based on the Ripley's K analysis (Fig. 2).

The Chi-Square analyses revealed that there was not a consistent association between specific habitat attributes and the clustering pattern of the egg mops. Although the majority of the habitat variables were significant associated with the distribution of egg mops across all spatial scales, the relative influence of those habitat variables changed across years and across scales (Table 1). In 2005, *D. opalescens* tended to deposit their eggs on the less complex substrate and the mops were associated with those habitats at finer scales. In 2006, there were fluctuations in the patterns of association but the influence of the habitat variables upon the distribution generally increased as the scale of the analysis increased, showing a pattern opposite to that seen in 2005. The distribution of egg mops in 2007 showed even less consistency in both the scale and habitat associations of the egg mops. Some variables had greater significance on egg mop distribution at the smaller spatial scales (i.e. TPI) while others increased in their relative influence as scale increase (i.e. slope). Other variables showed no clear patterns in their association with egg mop distribution and fluctuated in significance across scales.

3.4. Multibeam backscatter as a tool for detecting egg mops

Using the multibeam backscatter, we were able to identify areas of high egg mop abundance (Fig. 3). These areas were verified with the use of the drop camera. However, when we deployed the drop camera over areas where we could not see egg mops in the backscatter, there were smaller and more sparsely distributed egg mops that were not obvious in the backscatter.

4. Discussion

The acoustic remote sensing and video ground-truth methods employed in this study provided visual confirmation of a decrease in spawning activity in Monterey Bay and gave insight into the dynamic spawning patterns of *D. opalescens*. Based on their effectiveness as

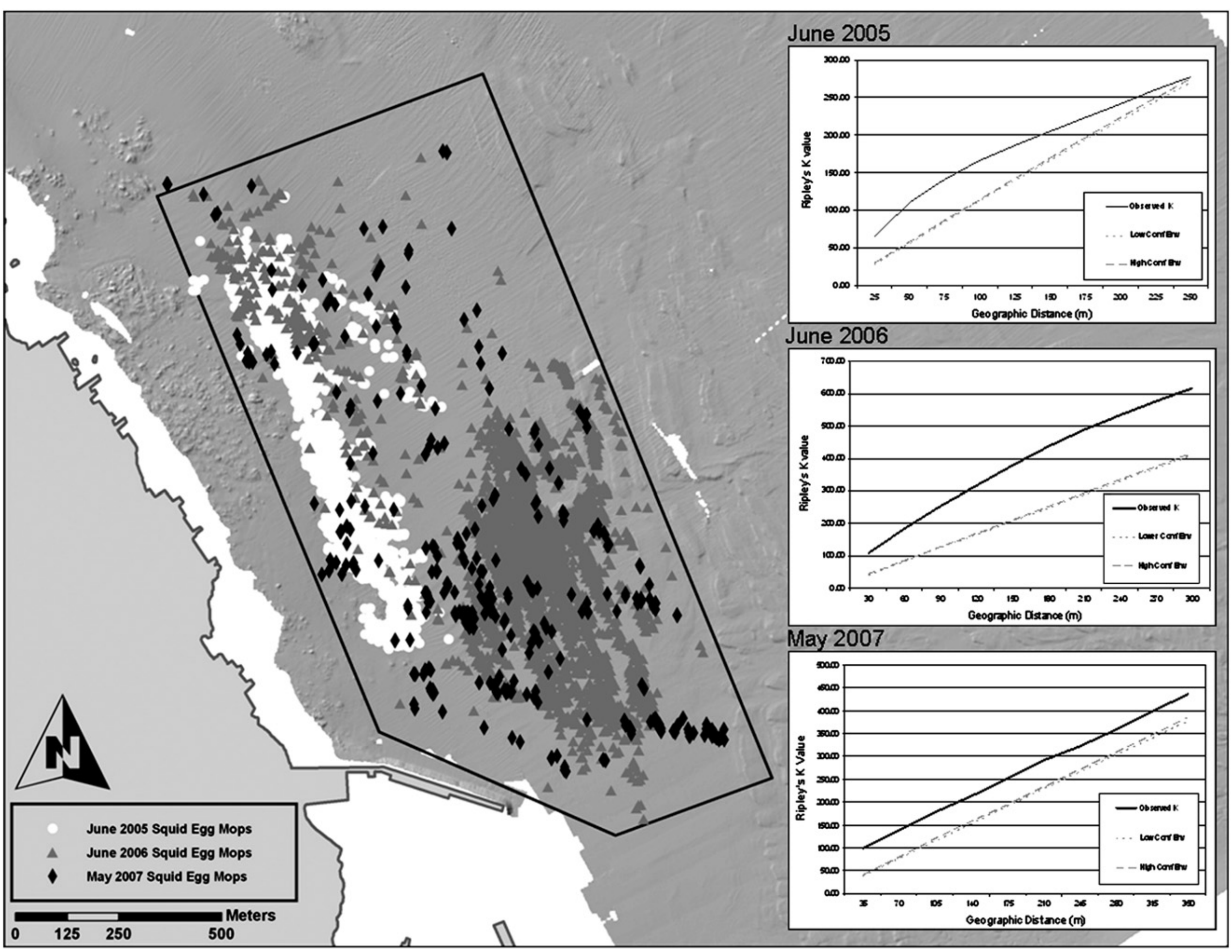

Fig. 2. Distribution of egg mops across all years in this study: white circles = June 2005 egg mops, gray triangles = June 2006 egg mops, and black diamonds = May 2007 egg mops. Plots of clustering pattern from the Ripley's K analysis are shown for each year. The solid black line displays the observed Ripley's K across all scales from 0 m to ~300 m. The Dashed lines show the 95% confidence envelope for complete spatial randomness.

Table 1
Residual values and test statistics for the Chi-Square tests used to determine the influence of variables to the distribution of egg mops across the survey area at four different scales for each habitat class (depth, VRM, slope, and TPI).

Year	Depth					VRM					Slope					TPI				
2005	Depth Class (m)	10 m	30 m	60 m	90 m	VRM Class	10 m	30 m	60 m	90 m	Slope class (°)	10 m	30 m	60 m	90 m	TPI Class	10 m	30 m	60 m	90 m
	14–16	−65.4	−60.6	−59.4	−29.4	0.00002–0.00004	107	107	99.0	125	1–2	−42.0	−46.0	−21.5	−7.8	4	107	107	99	125
	16–18	−19.4	−9.6	−7.4	−37.4	0.00004–0.00006	16.2	16.7	−32.0	9.3	2–3	34.0	49.0	1.5	48.3	5	16.2	16.7	−32	9.3
	18–20	94.6	91.4	64.6	138	0.00006–0.00008	−23.8	−17.3	17.0	−32.1	3–4	−2.0	−2.0	11.5	1.3	6	−23.8	−17.3	17	−32.1
	20–22	35.6	23.4	32.6	−5.4	0.00008–0.0001	−29.8	−26.3	−1.0	−18.0	4–5	10.0	−1.0	8.5	−41.8	7	−29.8	−26.3	−1	−18
	22–24	−45.4	−44.6	−30.4	−65.4	0.0001–0.00012	−32.8	−36.3	−44.0	−43.0		n/a	n/a	n/a	n/a	8	−32.8	−36.3	−44	−43
	Test Statistics					Test Statistics					Test Statistics					Test Statistics				
	Chi-Square	234	202	135	362	Chi-Square	308	328	331	486	Chi-Square	33	51	7	46	Chi-Square	304	328	331	486
	df	4	4	4	4	df	4	4	4	4	df	3	3	3	3	df	4	4	4	4
	Asymp. Sig.	0.000	0.000	0.000	0.000	Asymp. Sig.	0.000	0.000	0.000	0.000	Asymp. Sig.	0.000	0.000	0.060	0.000	Asymp. Sig.	0.000	0.000	0.000	0.000
2006	Depth Class (m)	30 m	90 m	180 m	360 m	VRM Class	30 m	90 m	180 m	360 m	Slope class (°)	30 m	90 m	180 m	360 m	TPI Class	30 m	90 m	180 m	360 m
	18–20	−19.0	−7.4	−4.8	−11.6	0.00002–0.00004	89.6	87.2	85.6	102	0–1	84.6	18.4	87.4	147.4	−2	−43.8	−43.8	−41.2	−41.2
	20–22	−14.0	−16.4	−31.8	−31.6	0.00004–0.00006	−9.4	−12.8	−22.4	9.8	1–2	36.6	100.4	20.4	−17.6	−1	−31.8	−35.8	−28.2	−43.2
	22–24	−1.0	−13.4	3.2	104	0.00006–0.00008	−21.4	−8.8	−29.4	−27.2	2–3	−36.4	−31.6	−22.6	−42.6	0	155.2	158.0	150.8	151.8
	24–26	39.0	52.6	55.2	−31.6	0.00008–0.0001	−21.4	−30.8	5.6	−40.2	3–4	−42.4	−43.6	−40.6	−42.6	1	−40.8	−38.8	−40.2	−43.2
	26–28	−5.0	−15.4	−21.8	−29.6	0.0001–0.00012	−37.4	−34.8	−39.4	−44.2	4–5	−42.4	−43.6	−44.6	−44.6	2	−38.8	−39.8	−41.2	−24.2
	Test Statistics					Test Statistic0073					Test Statistics					Test Statistics				
	Chi-Square	53	89	121	440	Chi-Square	258	239	261	334	Chi-Square	302	341	274	620	Chi-Square	689	715	661	673
	df	4	4	4	4	df	4	4	4	4	df	4	4	4	4	df	4	4	4	4
	Asymp. Sig.	0.000	0.000	0.000	0.000	Asymp. Sig.	0.000	0.000	0.000	0.000	Asymp. Sig.	0.000	0.000	0.000	0.000	Asymp. Sig.	0.000	0.000	0.000	0.000
2007	Depth Class (m)	10 m	60 m	180 m	360 m	VRM Class	10 m	60 m	180 m	360 m	Slope class (°)	10 m	60 m	180 m	360 m	TPI Class	10 m	60 m	180 m	360 m
	16–18	−7.6	−15.0	−44.8	−24.6	0.00002–0.00004	139	169	135.0	118	0–1	27.8	29.6	−3.8	131.0	−2	−50.2	−52.6	−44.8	−16.0
	18–20	15.4	17.0	18.2	65.4	0.00004–0.00006	3.8	−33.0	−30.8	12.4	1–2	106.8	114.6	114.2	10.0	−1	18.8	22.4	32.2	−41.0
	20–22	−36.6	−22.0	−1.8	−54.6	0.00006–0.00008	−34.2	−40.0	−0.8	−30.6	2–3	−24.2	−33.4	1.2	−48.0	0	115.8	112.0	114.2	62.0
	22–24	48.4	37.0	44.2	68.4	0.00008–0.0001	−52.2	−54.0	−45.8	−39.6	3–4	−43.2	−49.4	−39.8	−23.0	1	−53.2	−41.6	−51.8	−41.0
	24–26	−19.6	−17.0	−15.8	−54.6	0.0001–0.00012	−56.2	−42.0	−57.8	−60.6	4–5	−67.2	−61.4	−71.8	−70.0	2	−31.2	−40.6	−49.8	36.0
	Test Statistics					Test Statistics					Test Statistics					Test Statistics				
	Chi-Square	72	45	85	284	Chi-Square	381	528	393	336	Chi-Square	258	287	265	357	Chi-Square	313	303	361	214
	df	4	4	4	4	df	4	4	4	4	df	4	4	4	4	df	4	4	4	4
	Asymp. Sig.	0.000	0.000	0.000	0.000	Asymp. Sig.	0.000	0.000	0.000	0.000	Asymp. Sig.	0.000	0.000	0.000	0.000	Asymp. Sig.	0.000	0.000	0.000	0.000

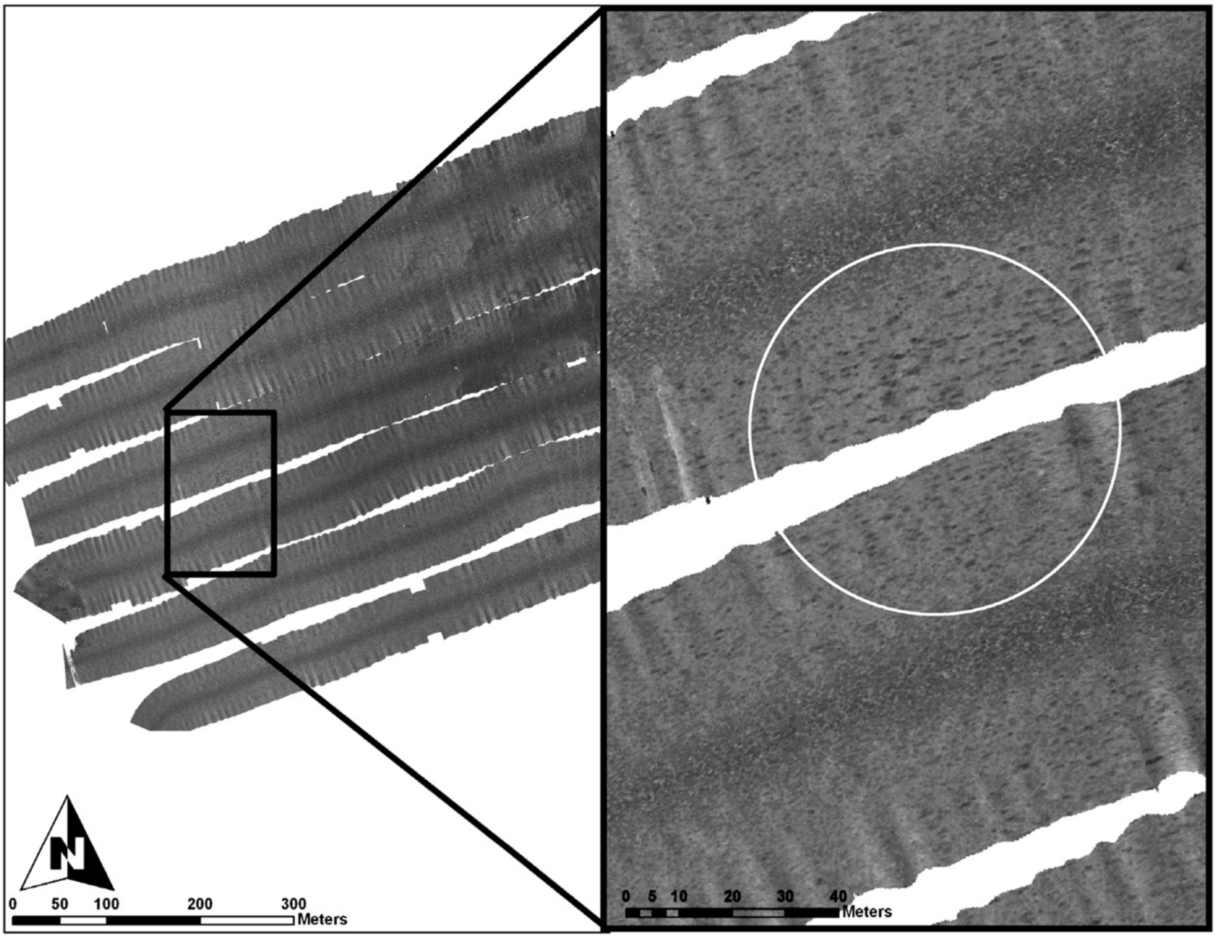

Fig. 3. The 0.20 m multibeam backscatter mosaic created from the Reson 7125 time series data collected in 2010 over a small area of the study site is shown in the left panel. On the right is a zoomed in portion of the mosaic. The dark splotches outlined by the circle in the image are dense aggregations of egg mops. The darker bands of data at the center of the swath are due to interference from the water column and egg mops can only be distinguished in the outer edges of the swaths.

comprehensive visualization tools, active and adaptive management policies that are needed to protect this species could use sidescan sonar as a tool to track spatial variation in the distribution and progression of *D. opalescens* spawning activities in key locations for spawning as well as fishing. The use of the towed sidescan sonar also provides for the accurate quantification of egg mops that could subsequently be used for the stock assessment of this commercially valuable species.

Previous studies have demonstrated that sidescan sonar is a useful tool for identifying squid egg mops on the sandy seafloor. Foote, et al. (2006) provided methodological details and demonstrated that sidescan can reliably detect and quantify squid egg beds. With the ease of collection and identification of squid egg mops within the resulting sonar mosaics, sidescan could prove to be a useful tool for the management of *D. opalescens*. It is an efficient tool for mapping large areas in a short amount of time (i.e. one day) and could be used to identify spawning areas throughout the duration of the season and over additional potential spawning areas, other than the small, commercially targeted spawning area used in this study. The resulting mosaics would be useful in predicting the current and subsequent populations, to set aside no-take areas, determine how many spawning areas are protected by MPAs already in place, or define catch limits for the management of the squid fishery either dynamically or statically.

In this study, towed sidescan sonar was used to accurately measure the abundance, distribution, and coverage of the egg mops within the study area. The first survey, in 2005, had both the greatest number of egg mops and the greatest coverage. The number of mops and area in the 2006 surveys had similar but somewhat reduced numbers. In 2007, however, there was a drastic decrease in both the number of egg mops and the total area of coverage. There was a general downward trend in the number of egg mops over the three years used in this study. Although this study does not have the data to address why this downward trend occurred, it was correlated with a downward trend in landings (California Department of Fish and Game, CDFG, 2010) and coincided with natural phenomena that were occurring during that time. Unusually warm years (2005–2007) were experienced by the North Pacific Gyro Oscillation (NPGO) (Bograd et al., 2009) and the introduction of a new predator, jumbo squid (Field et al., 2007), occurred within the time period of this study.

A decrease in the area of egg mops correlates with a decrease in total landings during the period of this study (California Department of Fish and Game, CDFG, 2010). With both the catch data and the sidescan data as evidence, it appears that the population of *D. opalescens* in southern Monterey Bay area fell to almost negligible numbers during the period of this study. However, 2010 has proven to be a successful year for market squid landings in the Monterey Bay fishery. In addition, a short survey of the study site showed that egg mops are in high abundance on the seafloor. Although we do not have evidence to fully understand the reason for the steep decline in *D. opalescens* during the time of this study, the change in ocean temperature between 2005 and 2007 (Bograd et al., 2009) could potentially explain the disappearance and reappearance of this species as was found by Reiss et al. (2004) in the Southern California Bight.

One shortcoming of this study is that additional surveys were not completed outside the project study area to determine if the squid were spawning in other locations. Smaller sporadic egg beds are known from Carmel Bay, but the egg beds in the study area off of Monterey have been well known for over a century. Also, if temperature was responsible for *D. opalescens* nearshore disappearance, they could have moved their spawning location to deeper depths (Reiss et al., 2004). The use of sidescan sonar to look for potential relocation of spawning grounds in similar habitats but different depth ranges could be helpful in further understanding the dynamic ecology of this species.

The depth distribution of squid eggs between all surveys was significantly different; however, the depth range of the total survey area was fairly limited. *D. opalescens* do have a depth preference for spawning (usually beyond the depths of kelp in the 20–60 m depth range (Hurley, 1977; Hanlon, 1998; Zeidberg and Hamner, 2002; Hanlon et al., 2004) but the analysis completed in this study shows that, even though they spawn in the same depth range, the depth distribution for spawning within that range changes from year to year. Not only was the depth distribution of egg mops different between years, it was also different within the same year. Results indicate that, although squids lay their eggs in the same general location, the exact area of egg deposition within the spawning grounds may change on an annual basis. Therefore, management strategies for this species will need to be as dynamic as its spawning patterns within any proposed management zone. Early season reconnaissance mapping, using sidescan sonar, could identify spawning locations and help to determine potential closure areas for subsequent squid fishing seasons. It has been well documented that loliginid squid, and *D. opalescens* in particular, are visually attracted to existing egg mops (e.g., Fields, 1965; Hanlon et al., 2004; Hixon, 1983; Hurley, 1977; Sauer et al., 1992). Upon encountering an existing egg mop males encounter a contact pheromone in the existing egg capsules (Cummins et al., 2011; King, et al., 2003) and compete for female mates, who lay egg capsules on existing egg mops. This aspect of squid reproductive biology suggests that any slight spatial variation in the initial laying of a single egg mop can radically alter the distribution of an entire population of egg mops on an annual basis. Thus sidescan sonar can be an effective tool to rapidly detect these spatial shifts in egg mop distribution prior to the beginning of a fishing season.

In addition to depth, the horizontal spatial distribution of *D. opalescens* tended to differ from one year to the next. The first year in this study, 2005, had a very limited spatial distribution of egg mops with the majority of spawning occurring in the shallow areas just beyond the kelp beds at the edge of the sand rock interface. During 2006, the majority of egg mops was clustered near the center of the survey area but there was a scattering of smaller clusters throughout. Then, in 2007, there was no noticeable clustering pattern and egg mops were widely distributed throughout the survey area with no large central concentration of egg masses (Fig. 2). From these observations it is clear that while *D. opalescens* do return to spawn in the same general area each year, the precise location (i.e. within a few hundred meters) of their egg laying within the well-known historical spawning area off of Monterey cannot be predicted in advance.

The chi-square analyses revealed that the relative contribution of each habitat variable to spatial patterns of egg mop clustering varied as a function of scale. Depth and vector ruggedness (VRM) had the most significant influence on the distribution of the egg mops for *D. opalescens* during the first year. In the following year; however, slope and TPI were more significant variables to the clustering pattern. In the third year (2007) the patterns were less clear and the variables varied in their significance over the different scales. Overall, egg mops are most commonly found in the mid-depth ranges (~25 m) and in areas of low complexity (flat, sandy areas) but the lack of clear association between the spawning patterns of *D. opalescens* and the habitat variables potentially responsible, make it difficult, if not impossible, to predict the exact location where the squid will spawn each season. Therefore, with dynamic management strategies in conjunction with modern mapping techniques, managers can move to protect critical habitat components whose importance to the persistence of the squid fishery can vary on an annual basis. As past studies have shown (Hixon, 1983), *D. opalescens* prefer to spawn in flat, soft sediment areas but, as shown here, do not appear to respond to subtle differences in the benthos throughout that habitat. Other variables, such as temperature, which were not explored in this study, may better explain the exact location where squid tend to spawn each year.

Through a short survey, we were able to demonstrate that backscatter data collected using a hull-mounted, multibeam sonar system, could serve as a reliable tool for defining *D. opalescens* spawning areas. Hull mounted multibeam systems allow for more accurate georeferencing of the data and are, logistically, much easier to run when compared to a towed sidescan system (Le Bas and Huvenne, 2009). In addition, the backscatter data are collected simultaneously with the multibeam depth data, which has proven useful for defining suitable habitats for spawning *D. opalescens*. Although the sonar is much farther from the seafloor and the egg mops are not as clearly defined as in the mosaics created from the towed sidescan sonar, the parallel use of a high resolution multibeam system could help in defining the main spawning areas. However, the higher-resolution data supplied by the towed sidescan is more useful when quantifying individual egg mops as well as smaller aggregations. With either system, there is a need for 100% overlap between the lines if full coverage mapping is desired. Since sidescan and backscatter systems do not collect useful data directly below the sonar, darker bands of interference can occur at the center of the swath, as seen in Fig. 3.

Complete baseline maps of known and potential spawning areas for *D. opalescens* would provide valuable information for defining spawning sites, and how locations can change seasonally during the spawning season, which in southern Monterey Bay is known to range from April to November, with a large peak in April/May and smaller one in September (Forsythe et al., 2004; Hixon, 1983). In addition, the application of more advanced survey techniques, such as the use of autonomous underwater vehicles (AUVs), would help to collect sidescan and photographic data with finer and more consistent resolution to aid in the identification and quantification of egg mops.

5. Conclusions

The ability to accurately map the spawning sites of *D. opalescens* could be very useful in shifting the monitoring of this commercially important species to a dynamically managed fishery. Because they do not show a strong association with specific habitat features, we are unable to predict exactly where they will spawn each year. Therefore, the use of sidescan sonar or multibeam backscatter data to define the seasonally variable spawning locations could help in setting aside dynamic or static no-take areas. In addition, the ability to quantify the egg mops could lead to biomass estimates of this species and, eventually, the methods used in this study could help with stock assessments of the species.

Acknowledgements

We would like to thank Dr. Ken Foote of Woods Hole Oceanographic Institution for his aid in the collection of the data used in this project. We would also like to thank members of the Seafloor Mapping Lab at California State University, Monterey Bay for their help with both data collection and processing. The authors are grateful for funding from the National Sea Grant, Essential Fish Habitat Program, and especially the interest of program manager Emory Anderson, Sea Grant Project No. NA16RG2273. **[RH]**

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